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The Cranial Osteology of the New World Tyrannoidea and Its Taxonomic Implications.

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THE CRANIAL OSTEOLOGY OF THE NEW WORLD TYRANNOIDEA AND ITS TAXONOMIC IMPLICATIONS

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ABSTRACT

The six families of Neotropical tyrannoid passerine birds, comprised of over 500 species in approximately 180 genera, constitute a major portion of the avifauna of South and Central America. The last major revision of this group was completed more than 35 years ago.

In an effort to provide at least partial solutions to some of the existing systematic problems, a survey of the cranial osteology of members of these families was undertaken. Nearly 1200 skulls of 224 species, comprising 117 genera, were examined.

The skulls examined were placed within morphological groupings that seem to correspond closely to groupings based on other known biological features of the birds.

Characters of the feet and legs had been relied upon previously to place within families the birds for which the more basic anatomical features were not known. Some of these placements have seemed incorrect to many ornithologists but no other information was available for evaluation of these allocations. The skull, in combination with general appearance, food habits, and breeding behavior (insofar as is known), seems to provide a character complex that helps to clarify relationships among this difficult

group of birds.

Skulls of the flycatchers (Tyrannidae) are relatively uniform when compared to those of the Cotingidae. Several types of skulls occur within the diverse family Cotingidae; these types correspond to some of the subfamily groupings which, although widely used in the last century, have now disappeared from the literature. The use of several of these subfamilies--Attilinae, Tityrinae, Cotinginae, Gymnoderinae, and Querulinae--is reinstituted. A new subfamily is erected to contain the bellbirds (Procnias).

Skulls of most of the manakins (Pipridae) are barely distinct from those of the Cotinginae, but the retention of the family is suggested since most of its members possess an elaborate method of courtship not yet found so well developed among the Cotingidae.

The skulls of birds of the monotypic families Rupicolidae, Phytotomidae, and Oxyruncidae were all found to be highly specialized and provide no evidence for uniting any of these birds with any other family.

Skulls of the cotingas Attila, Pachyramphus, Platypsaris, Rhytipterna, Erator, and, to a lesser extent, Tityra are flycatcherlike. The mourners (Rhytipterna) are transferred to the Tyrannidae, and the reallocation of the other genera is discussed.

INTRODUCTION

Although birds are probably the most thoroughly studied class of vertebrates, the foundation on which avian classification rests in many cases is not substantial. The ornithologist is only too aware of the inadequacies that exist at all levels of the present system, particularly with regard to the taxa above the genus.

For the ornithologist, the suboscine passerines have always been one of the most taxonomically difficult groups with which to work. Tropical faunas are characteristically composed of great numbers of often closely related species. The suboscines are no exception. They are a group of families presumably of tropical origin and, for the most part, depend on the most abundant animal group, the insects, for their livelihood. They have undergone extensive adaptive radiation until, along with the oscine passerines, they have come to constitute the largest ordinal assemblage in the avifauna of the New World. In spite of this great radiation and the consequent large number of morphological variations that occur within the group, compared with other avian orders, these families have remained peculiarly homogeneous at least in regard to their more

superficial morphological resemblances.

The great strides that ornithology has taken within the last few decades have not been directed along lines that would provide the criteria necessary for the determination of relationships among the closely related groups of such an aberrant group of vertebrates as the birds. From the time of the very first arrangements of the genera within these families, systematists have been aware that insufficient knowledge was available of any but the most superficial criteria. Especially with the largest family, the Tyrannidae, each of the workers who has attempted anything approximating a monographic treatment of the family has failed completely even in defining adequately all the genera. No one has been willing to depart radically from the earliest arrangements carried over from the middle of the last century. Each has professed the desire for more information of the sort that would shed more light on the true relationships within the family, and among the neighboring families as well, so that his own artificial arrangement might be improved.

The reasons for this state of affairs lie within the history of both the development of ornithology as a science and the evolution of the birds themselves. The fact is little realized that since the extensive investigations by the great anatomists of the last century--Gadow, Fürbringer, Garrod, Forbes, and their contemporaries--there

has been little added to our knowledge that would enable us to improve extensively on their work. This paucity of information has not allowed really satisfactory delimitations of even the higher taxa of birds.

At a time in which most vertebrate higher taxa were already established on most of the continents, the major radiation of passerine birds is not believed to have yet occurred, so that at the present stage in avian evolution a number of these families still are confined to the continents of their origin. The New World--particularly Central and South America--was one of the most poorly known faunistic regions during the time in which the early anatomists were working. Some of the family groupings of passerine birds (more recently evolved than other orders, or so it is generally held), including the majority of the suboscines, are endemic to South America. Accordingly, these groups were poorly known and few specimens were then available for investigation. The work of the pioneer anatomists was not continued to any significant extent by others, and the emphasis in ornithological studies shifted away from anatomy. When these facts are made clear, we are able to understand the reason for the inadequacies that persist in avian classification.

Even the simple addition of facts to the body of ornithological knowledge is not sufficient to provide adequate solution to the problems facing the student of avian

relationships, for no one has yet demonstrated satisfactorily what is to be done with these facts once they have been gathered. We do not yet have a body of knowledge sufficient even to allow us to decide unequivocally which of the already known characteristics can safely be used as diagnostic criteria.

In the face of the incompleteness of our knowledge of the anatomical features that should provide the logical starting plac for a natural classificatory scheme within the Passeriformes, there is the added complication of a growing awareness of the adaptive nature of many anatomical features and the consequent unsureness as to which features are the most indicative of relationships. The further realization that other features of the organism than those of a purely anatomical nature may well be of equal importance in the ascertainment of phylogenetic affinities gives us a better appreciation of the role played by the morphological characters, but not necessarily a stronger foundation upon which to base conclusions. Not until a more complete knowledge of the internal characters sought by the old anatomists is added to our knowledge of the inadequate external characters upon which the present classificatory schemes of the suboscine Passeriformes are based, will we be reasonably certain even of which birds to include within the families.

To the last must eventually be added more subtle

information of a general biological nature before a really close approach can be made to a thorough natural scheme of classification for this diverse group. Such a scheme may never be devised, for, in addition to the limitations inherent in human insight, profitable investigations are being conducted at so slow a rate that it is entirely possible that the inroads of civilization may bring about the reduction or alteration of the natural habitats of many species before the necessary biological information can be gathered.

For the present, at least, the development of a realistic and accurate system of classification seems to be dependent upon a foundation provided by purely anatomical studies. The need for studies of this nature has been stressed by Mayr (1955) and Stresemann (1955).

Some time ago I began a study of the adaptive modifications in the Neotropical family Tyrannidae. As the study progressed, I became increasingly aware that some of the differences noted among supposedly closely related forms might not be attributable solely to adaptive radiation and that such a study could not be properly conducted without a more thorough appreciation of the relationships of the birds concerned. Accordingly, this study was undertaken in an attempt to provide at least a partial solution to the problem. During the course of the ensuing investigation the need for expanding the study to include

the closely related families Cotingidae and Pipridae became evident, since no clear lines of demarcation could be determined for the family. For completeness, the three remaining families of the Neotropical Tyrannoidea, Rupicolidae, Phytotomidae, and Oxyruncidae, all monotypic, were also included.

In all, 1182 specimens of 226 species of 117 genera have been examined (Appendix I). Of the 175 currently recognized genera, skulls of species of only 10 have been previously described in an adequate fashion.

Surveys of a number of other morphological features were made (e.g., postcranial osteology, tarsal scutellation, and modifications of primary wing feathers). Mention of the latter information has not been included except where pertinent.

In a further effort to gain a better perspective of the families in question, I also examined 56 genera from among the Neotropical families of the superfamily Furnarioidea that, together with the Tyrannoidea, comprise the suborder Tyranni. Representative Old World genera of the remaining suboscine suborders Menurae and Eurylaimi were also examined (Appendix II).

A detailed presentation of the cranial osteology of the Furnarioidea, being beyond the scope of this survey, is planned for a later date. Because of the relative homogeneity of the furnarioid skulls, I was able to construct a

workable preliminary key to the families of that group. The skulls of the flycatchers, cotingas, and manakins, as these families are presently constituted, presented such an array of modifications and overlapping skull types that it was impractical to extend the key any further into the Tyrannoidea than the Phytotomidae, Oxyruncidae, and Rupicolidae. The key is presented below:

PRELIMINARY KEY TO THE SKULLS OF THE NEW WORLD FAMILIES OF THE SUBORDER TYRANNI

1a. Lacrymal partly or completely fused (absent?) to ectethmoid (superfamily Furnarioidea) 2

1b. Lacrymal free (superfamily Tyrannoidea). 5

2a. Lacrymal partly or completely fused to ectethmoid, more or less recurved anteromedially in front of ectethmoid; ectethmoid partly or wholly detached from frontal; nares enlarged . . . . . Family Rhinocryptidae (=Pteroptochidae)

2b. No evidence of lacrymal; ectethmoid united to frontal; nares not enlarged. 3

3a. Nares conspicuously constricted posteriorly ("narrowly pseudoschizorhinal") . . . . . .Family Furnariidae

3b. Nares never conspicuously constricted posteriorly, always holorhinal or amphirhinal. 4

4a. Interorbital septum fully ossified (imperforate); nares holorhinal (never amphirhinal but often

"broadly pseudoschizorhinal") . . . . . .
. . . . . Family Dendrocolaptidae

4b. Interorbital septum largely unossified (perforate); nares basically holorhinal, walls of nasal capsule ossified (amphirhinal) except in Formicarius and Conopophaga . . . . . .Family Formicariidae

5a. Bill fringilloid; rows of tubercles on palatal surface of premaxillae. . . . . Family Phytotomidae

5b. Bill otherwise; tubercles absent. 6

6a. Bill icteroid; frontonasal hinge elevated above level of head of lacrymal . . . .Family Oxyruncidae

6b. Bill various; if slender, frontonasal hinge at level of lacrymal 7

7a. Nasal capsule ossified, amphirhinal or secondarily holorhinal; inferior turbinal (maxilloturbinal) larger than, or equal to, alinasal turbinal (atrioturbinal); vomer tubular . . . . . .
. . . . . .Family Rupicolidae

7b. Nasal capsule unossified, or if ossified, alinasal turbinal larger than inferior turbinal; vomer U-shaped or flat. . . . . .Families Cotingidae, Pipridae, Tyrannidae (including Corythopis)

Users of Ridgway's "Key to the Families of Mesomyodi" (Ridgway, 1907: 330-332) will find that discrepancies exist between his key (in which a few osteological characters are given) and the one presented here. Ridgway, in

construction of his key, attributed schizorhinal nares to the Formicariidae and holorhinal nares to the Furnariidae, but the reverse is actually true. The "Key to the American Families of the Mesomyodi" in Helimayr (1924: 1-2) is based on that of Ridgway, and the same errors appear. In addition, there has been a transposition of sternal characters, a four-notched sternum being assigned to the Formicariidae, and a two-notched sternum to both Pteroptochidae (=Rhinocryptidae) and Conopophagidae.

Peter Ames and Mary Heimerdinger, in a paper presented before the American Ornithologists' Union in 1964, demonstrated that the two genera of the furnarioid family Conopophagidae differed in characters of the syrinx, sternum, and pterylosis. In addition, the diagnosis of a four-notched sternum for Conopophaga was shown to be inaccurate. They recommended transferrence of Corythopis to the Tyrannoidea, tentatively within the Tyrannidae, and suggested that the affinities of Conopophaga lie with the Formicariidae. Users of the preceding key will note that skulls of these two genera "key out" in accordance with the recommendations of Ames and Heimerdinger.

Prior to the late Nineteenth Century, the Furnariidae were included as a subfamily in the Dendrocolaptidae. Ridgway (1911), in accepting the earlier separation of the Furnariidae by Stejneger (1885), characterized the two families by features of the skull (nares and other

characters) and the structure of the feet.

In a paper written in response to Ridgway's action, von Ihering (1915) demonstrated that the pseudoschizorhinal naris (in its most "technical" sense) exists to some degree in enough forms of both groups to render it valueless as a single diagnostic character. If for practical use alone in the foregoing key, the term schizorhinal (pseudo-schizorhinal) is restricted to the condition in which the naris is conspicuously narrowed posteriorly, couplet 4 in the key will work for most skulls (except those of Xenops and possibly others that I have not examined).

Correlated modifications of the foot and tail, such as those that occur in the Dendrocolaptidae, have been shown to be associated with tree-trunk foraging (Richardson, 1942, and others).

If the present generic allocations are correct (which they may not be), the presence of forms intermediate between the two groups in external, as well as in a number of cranial characters, makes it evident that evolution within the dendrocolaptid-furnariid assemblage has not proceeded to a level at which a clear-cut line of demarcation can be drawn. On a comparative basis with the other furnarioid groups examined, there does not seem to be a solid foundation for a family-level distinction between the two groups. If the present families are to be maintained, the erection of a higher category to contain the Dendrocolaptidae and

Furnariidae would seem to be necessary to emphasize the distinctness of these two closely related groups of birds from the remainder of the Furnarioidea.

CLASSIFICATION OF THE TYRANNOIDEA

I have accepted as a working arrangement the allocation of families and genera of tyrannoid forms in the Catalogue of Birds of the Americas and the Adjacent Islands (Hellmayr, 1927 and 1929). The taxa above the family level used in this study are those adopted by Mayr and Amadon (1951) and Wetmore (1960).

Hellmayr's arrangement of subfamilies and genera of the Tyrannidae is based largely on the classifications of Sclater in the Catalogue of Birds in the British Museum (1888) and Berlepsch (1905). Sclater's classification is derived from Cabanis' Museum Heineanum (Cabanis and Heine, 1859) by way of the Nomenclator Avium Neotropicalium (Sclater and Salvin, 1873).

Prior to the appearance of Hellmayr's arrangement, Ridgway (1907) had monographed the North American representatives of the tyrannoid assemblage, incorporating some of Berlepsch's modifications of von Ihering's (1904) arrangement of tyrannid subfamilies, and making a number of other changes. For reasons discussed in a later section of the present work, Hellmayr was unable to accept Ridgway's alterations, but he does seem to have accepted many of von Ihering's recommendations.

Attempts at the classification of birds prior to that of Cabanis are summarized by Gadow (1896), Sharpe (1891), Newton and Gadow (1896), and Newton and Mitchell (1911). For modern discussions of problems in suboscine classification other than those discussed in later sections of this work, see Mayr and Amadon (1951) and Amadon (1957).

The following is an outline of the principal nonosteological "internal" characters used by authors in the basic classification of the Tyrannoidea. It must be remembered that these characteristics for most genera are merely assumed.

Suborder Tyranni (Mesomyodes, Clamatores)

Syrinx "mesomyodean," intrinsic muscles (if present) attached to middle or either end (but not both ends) of bronchial semirings.

Superfamily Furnarioidea (Tracheophonae)

Syrinx "tracheophone" (tracheal), muscles attached to middle of bronchial semirings.

Family Dendrocolaptidae, Woodcreepers

Furnariidae, Ovenbirds

Dendrocolaptidae and Furnariidae have two pairs of tracheobronchial muscles, Formicariidae and Rhinocryptidae one.

Formicariidae, Ant-thrushes, Antbirds

Conopophagidae, Antpitpits

Rhinocryptidae, Tapaculos

Superfamily Tyrannoidea (Haploophonae)

Syrinx "haploophone" (bronchotracheal), intrinsic muscles attached to one end of bronchial semirings.

Family Cotingidae, Cotingas and allies

Pipridae, Manakins

In Cotingidae and Pipridae the principal artery of the thigh is the femoral; in all other passerines it is the sciatic (ischiatic).

Phytotomidae, Plantcutters

Rupicolidae, Cocks-of-the-rock

Tyrannidae, Tyrant Flycatchers

Oxyruncidae (Oxyrhamphidae), Sharpbills

Tyrannidae and Oxyruncidae have the intrinsic muscles of the syrinx inserted on the dorsal ends of the bronchial semirings ("anacromyodian"); all other Tyrannoidea, except Philepittidae, have the muscles inserted on the ventral ends of the bronchial semirings ("catacromyodian").

Pittidae, Pittas

Acanthisittidae (Xenicidae), New Zealand Wrens

Philepittidae, Asities, False Sunbirds

Syringeal muscles not attached to bronchial semirings.

Detailed biological information necessary to supplement the present essentially morphological classification has been slow in forthcoming. Nevertheless, there is enough fragmentary information available to allow broad tentative generalizations to be applied to the better defined groups and subgroups of tyrannoid birds. Much of this information is contained in such works as Bent (1942), Gilliard (1962), Goodall, et al. (1957), Hudson (1920, 1951), Koepcke (1954a, 1954b, 1958), Marelli (1919), Miller (1963), Mitchell (1957), Selva (1917), Sick (1959), Skutch (1946, 1949, 1954, 1960), Slud (1960, 1964), B. K. Snow (1961), D. W. Snow (1962a, 1962b), Swainson (1862), von Ihering (1904), and Wetmore (1926).

Additional fragments of information have been gleaned from numerous distributional surveys and from conversations with other ornithologists who have encountered some of these birds in the course of their experience in the field.

There appear to be two major divisions within the New World Tyrannoidea, one composed of those birds that are exclusively or primarily frugivorous, and the other of those that are exclusively or primarily insectivorous.

The fruit-eaters (cocks-of-the-rock, manakins, cotingas, bellbirds, fruitcrows and their allies) tend to an increase in size, a loss or reduction of rictal bristles, a compression of the bill, and a development of elaborate courtship displays that are generally more or

less communal on the part of the males.

In correlation with the elaborate courtship displays (usually some form of "arena" or "lek" behavior), males acquire conspicuous coloration and ornamentation in the form of caruncles, wattles, and feather modifications. Females usually seek out and choose among the displaying males, and then, after a brief pairing, they leave their mates and raise their young alone.

Foraging behavior is difficult to assess, since the birds are most often seen either in courtship display or else aggregated or congregated in fruit-laden trees. These situations may represent opposite extremes, since it appears that at other times many of these birds are "passive foragers," remaining quietly in dense brush or high forest canopy, thus often escaping detection by the human observer.

The insectivores (tityras, becards, attilas, and flycatchers) tend to a reduction in size, and to either an increase in development of rictal bristles and a depression of the bill (aerial insect-chasers) or a reduction in rictal bristles and a compression of the bill (terrestrial hunters, foliage gleaners). Foraging behavior tends to be "passive" in the case of the former (perching quietly for varied periods of time, occasionally "sallying" for insects in the air or on the surface of leaves), and "active" in the case of the latter (searching for insects or other

animal prey on the ground or in foliage or brush).

Plumages tend to be inconspicuous. Single males court the females, forming pair-bonds of varying duration and remaining more or less in attendance during all or part of the period of nest-building, incubation, and rearing of the young.

Some of the above generalizations are summarized in Table I, correlated with the skull types that will be enumerated later.

TABLE I. Generalized Correlations of Skull Types with Feeding Habits and External Features. Symbols: Bill shape--C, compressed; D, depressed; S, swollen. Rictal bristles--A, absent; S, strong; W, weak. Foraging habits, column 1--A, active; P, passive. Foraging habits, column 2--A, aerial; F, foliage; P--predatory; T, terrestrial. Coloration--B, bright (conspicuous); D, dull (cryptic?). Principal food preference--S, smaller fruits (berries, etc.); F, larger fruits; I, insects; L, leaves; O, omnivorous (fruits and insects); V, small vertebrates; ( ), primary preference.

Skull type	Group	Bill shape	Rictal bristles	Foraging habits		Color-ation	Food preference
IA	Fluvicolinae	C,D	S-W	A,P	T-A-P	B	I,V
	Tyranninae	D	S	P	A	D	O (I)
	Myiarchinae	D	S	P	A,F	D	I
	Platyrinch-inae	D	S	A	F	D	I
	Euscarthminae	D	S-W	A	F	D	I
	Serpophaginae	C	W	A	F	D	I
	Elaeniinae	C	W	A	F	D	I[1]
IB	Attilinae	C	S	P	A-F-P	D	I,V
IC	Tityrinae	D,S[2]	S-W	P	A-F	B,D	O (I)
IIA	Pipridae	C	A-W	A?	F	B	O (B)
IIA	Cotinginae	C	A-W	P	F	B	B
IIB	Gymnoderinae	C	A	P	F	B	F
IIC	Pipreinae	C	A	P	F	B	F
III	Querulinae	C[3]	S	P	F	B[4]	O (B,F)
IV	Rupicolidae	C	A	F?	F?	B	F
V	Phytotomidae	C	A	A	F	B	L
VI	Oxyruncidae	C	A	?	F	D	?

[1] Elaenia, O (B).
[2] Tityra (s.s.), C,S.
[3] Querula, C,S.
[4] Lipaugus, D.

DESCRIPTIONS

Introduction

The tyrannoid skulls examined in this survey have been grouped together in types for convenience in description. Among the divisions of the Tyrannoidea a number of genera have skulls very similar to those in other taxonomic categories. To avoid duplicate or otherwise repetitive descriptions, these genera are so designated and descriptions of these skulls are included in the types they most closely resemble. Only the differing features are enumerated.

A general description of the most pertinent features precedes the descriptions of individual types. The flycatchers are sufficiently alike that the general description suffices for the family with tabulation alone of differing characters being necessary for each genus examined. Other tyrannoid types are different enough that a more complete treatment is needed for most.

General Description

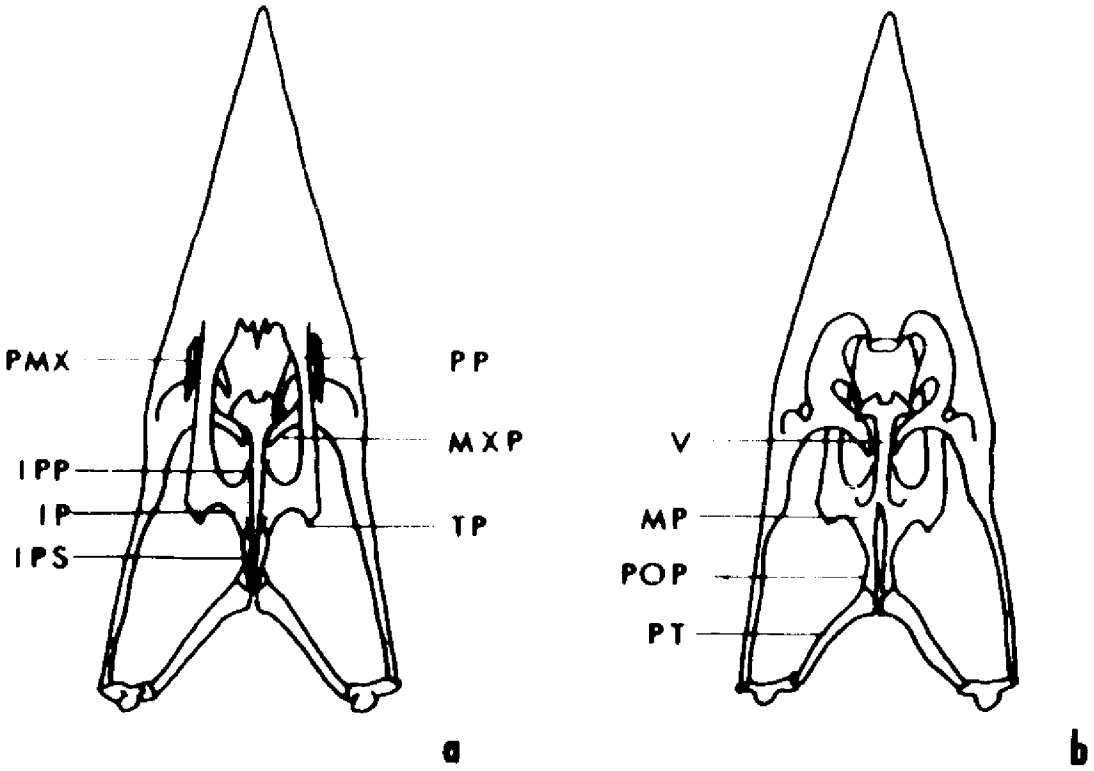
The <u>interorbital septum</u> in birds is attributed by most authors to the "ethmoid complex" and considered to be the mesethmoid. The dorsalmost portion is believed to be

contributed by the frontals that roof the orbit. The tyrannoid septum (Figure 3, Type 3), in its least ossified condition, is perforated by two fenestrae, the superior and inferior interorbital fenestrae, that extend the length of the orbit and merge posteriorly with the olfactory and optic foramina, respectively. In many cases the inferior fenestra is obliterated by ossification (Figure 3, Type 2) and, in still others, both are ossified (Figure 3, Type 1). The superior fenestra coincides with that portion of a more completely ossified septum that, in some cases, exists between the tracts of the olfactory nerves, which run exposed within the orbits from their points of emergence in the rear of the orbits to the nasal capsule. The mesethmoid is fused ventrally with the parasphenoidal rostrum.

The anterior wall of each orbit is composed of a near-vertical plate, the ectethmoid (Figure 1, EE), that is expanded laterally above and below. The dorsal extension, or arm, fuses above with the frontal, leaving a foramen medial to it, the ectethmoid foramen, that allows the passage of the olfactory nerve from the orbit into the nasal capsule. The ectethmoid plate is usually flattened, but the lower extremity of the ventral arm is often enlarged at the tip.

The rear wall of the orbit merges laterally with a depression on the side of the cranium, the temporal fossa (Figure 1, TF), which is bordered above by the postorbital

Figure 1. Cranial Features of Tyrannus dominicensis. Figure 1a, palate (ventral); b, palate (dorsal, cranium removed); c, lateral aspect (cranium raised). Symbols: EE, ectethmoid; IOS, interorbital septum; IP, interpalatine; IPP, interpalatine process (spur); IPS, interpalatine scroll; L, lacrymal; MP, mediopalatine; MXP, maxillopalatine; NS, nasal septum; POP, postpalatine; PMX, palatomaxillary; PP, prepalatine bar; PT, pterygoid; Q, quadrate; QJ, quadratojugal bar; TF, temporal fossa; TP, transpalatine; V, vomer.


PMX
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MXP
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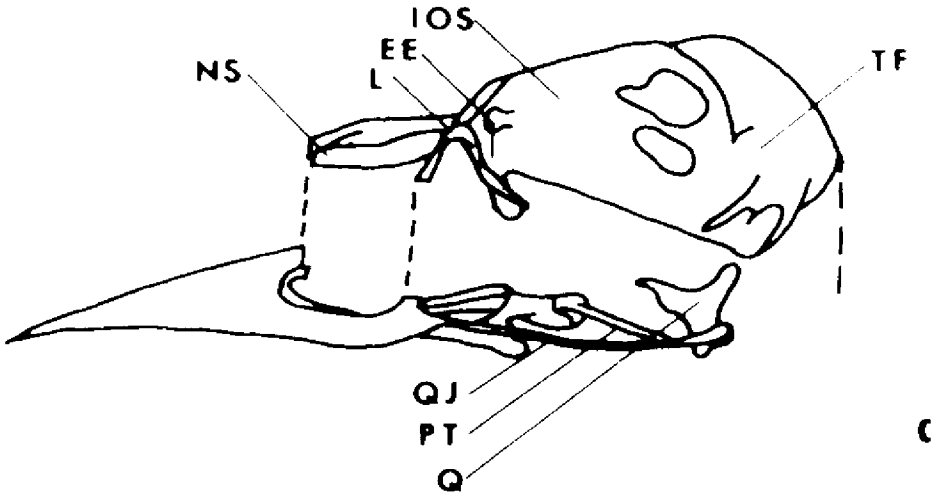
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process and below by the zygomatic process. The temporal fossa and zygomatic process are areas of origin in many passerines for the adductor muscles that have the principal function of raising the lower jaw. The postorbital process serves as the cranial point of attachment of the postorbital ligament that binds the mandible to the skull.

Lateral to the ectethmoid is the lacrymal (prefrontal of some authors). Typically it is a small bone expanded above and below (Figure 1, L). The dorsal portion, or head, nestles in the space between the frontal and the maxillary process of the nasal. The lower portion, or foot, is expanded laterally and rests on an expansion of the maxillary contribution to the quadratojugal arch.

The paired palatines (Figure 1) are the most complex bones in the avian skull. They serve as the origin for most of the elements of the compound pterygoideus muscle, the elements of which accomplish retraction and depression of the palate and upper mandible.

The portion of each palatine lying alongside the parasphenoidal rostrum (basisphenoidal rostrum of some authors) is the mediopalatine. An ectethmoid process proceeds anteriorly to fuse with a crura of the vomer. The mediopalatine runs posteriorly as the postpalatine process, the principal articulation with the pterygoid. The mediopalatine also extends ventrolaterally and is based by a transverse interpalatine plate.

Medially, the interpalatine has an anterior pointed interpalatine process or "spur." Laterally, the interpalatine has both an anterior and a posterior extension. The anterior extension is the long, flat prepalatine process, or prepalatine bar, that fuses with the premaxillae at the anterior end of the nasal cavity. The posterior extension is the transpalatine process.

In tyrannid skulls the pre-, trans-, and interpalatines are the most variable elements of the palatines. The prepalatines vary in width and in degree of curvature and of anterior convergence. The transpalatines vary considerably both in length and in width. Each interpalatine generally projects ventrally along its medial edge, the plate thus formed sometimes becoming curved laterally along its lower border in a scroll-like fashion.

The vomer (prevomer of some authors) is a single median bone (Figure 1, V) formed by the fusion of paired vomerine cartilages with each other and with a small number of other elements (see Parker, 1875, for a complete discussion). The posterior portions of the paired vomerine cartilages remain separate and each crura fuses with the ethmoid process of the palatine behind it. The free end of the vomer, when viewed from below, is bicornuate. The "horns" are attributed by Parker (op. cit.) to "septomaxillaries," separate ossification centers that fuse with the vomer early in development. Each of the horns is

often more or less expanded above as a projecting plate that is subtended by an incompletely ossified area where the alinasal turbinals articulate with the vomer. Ventrally, the vomer bears on its free end two tubercles that serve as articular processes that join with the anterior margins of the maxillopalatines.

The pterygoid (Figure 1, PT) extends obliquely from its articulation with the quadrate to the parasphenoidal rostrum where it articulates with the postpalatine process of the palatine, forming the palatopterygoid joint. The anterior end of the tyrannid pterygoid is expanded into a short plate (pterygoid footplate) that is usually separated from the palatine by a more or less vertical suture. In other tyrannoids, the footplate may be long and separated by an oblique suture. This variation may be due to the fusion of a separate anterior pterygoid center of ossification (see Pycraft, 1901, and Jollie, 1958) with the postpalatine in the first instance, or with the "posteropterygoid" in the second.

The paired maxillopalatine processes (Figure 1, MXP) extend from the maxillae towards the vomer and articulate with the ventral surface of that bone. They are basically straplike and more or less curved posteriorly either alongside or beneath the shaft of the vomer. They may be instead more or less triangular, curved to a varying degree, and may be either blunt or acute at the apex. The

triangular form owes its greater breadth to ossification of the base of the nasal wall along the anterior edge of the basic strap-shaped process (see section on nasal region).

Alongside the lateral surface of the anterior end of each of the prepalatine bars there is in many cases a spur-like process arising from the ventral surface of the palate. This process is the palatomaxillary (Figure 1, PMX), considered by Jollie (1958) and Bock (1960) to represent the embryonic palatine process of the premaxilla. The absence of this structure is taken by most authors to be an indication of fusion with the prepalatine. Problems surrounding the interpretations of the palatomaxillaries will be dealt with in a later section.

The nasal capsule is ossified in a number of genera. It is described in detail in a later section.

Type I Skulls

A. Flycatchers (Tyrannidae)

Genera included: 85 genera examined (see Table II).

Illustrations: Tyrannus (palate), Figure 1; nasal septa, Figure 2; interorbital septa, palatines, crania, Figure 3; Myiarchus (nasal capsule), Figure 6, Figure 8a.

Previous descriptions and illustrations: Elaenia sp., Parker, 1875: 330-331; Plate LXI, Figures 1, 2. Muscisaxicola mentalis, Parker, 1875: 323; Plate LIX, Figures 9, 10. Myiarchus crinitus, Shufeldt, 1889,

Figure 2. Types of Nasal Septa. Left column, cross-section; center column, ventral aspect; right column, lateral aspect (all illustrations diagrammatic). For further explanation, see p. 69.

Type:

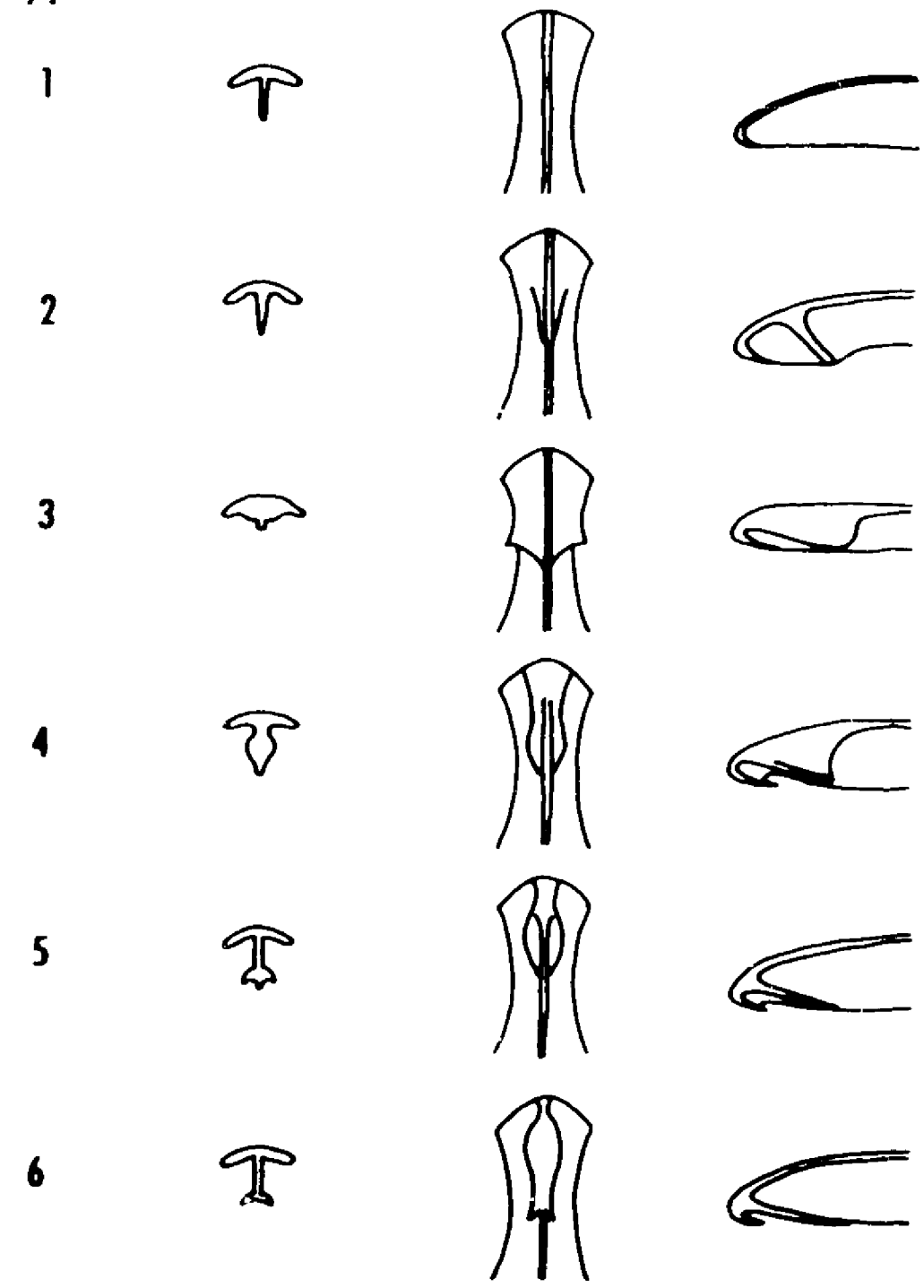
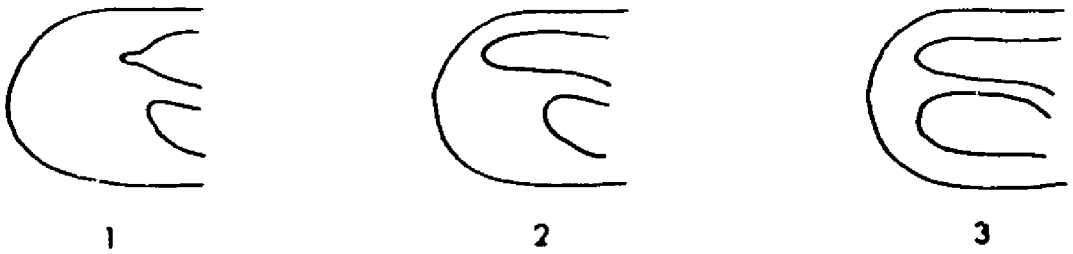


Figure 3. Features of Type I Skulls. A, types of interorbital septa; B, types of palatines; C, types of crania (posterior aspect).

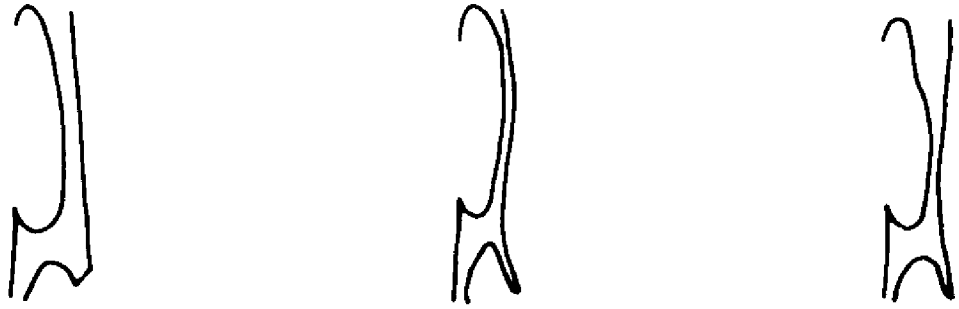
A



1 2 3

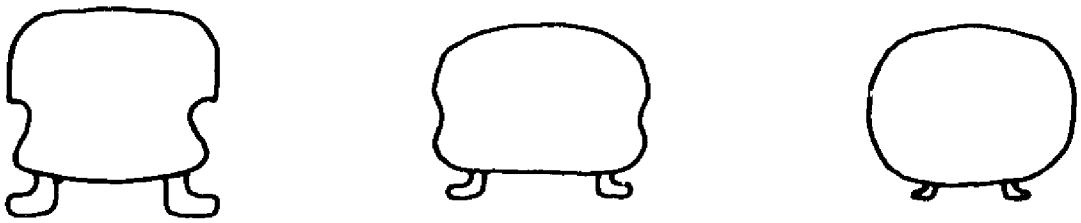
4 5

B



1 2 3

C



1 2 3

TABLE II. Variable Characters of Flycatcher Skulls. Numbers in columns refer to "Types" illustrated in Figures 2 and 3. Column I--Nasal septum. Column II--Interorbital septum. Column III--Palatines. Column IV--Cranium. Column V--Palatomaxillaries (+ = present).

Genus	I	II	III	IV	V
FLUVICOLINAE					
Agriornis	6	2	1	1	+
Xolmis	6	2	1	1	+
Muscisaxicola	6	2	1	2	+
Lessonia	6	3	2	3	+
Myiotheretes	6	?	1	1	+
Neoxolmis	6	2	1	1	+
Ochthoeca	6	2	2	2	
Savornis	6	2	3	2	+
Colonia	6	1	2	2	
Gubernetes	6	1	1	1	
Yetapa	6	1	1	2	+
Knipolegus	6	2	1	2	
Entotriccus	6	2	2	2	
Lichenops	6	3	2	2	+
Fluvicola	6	3	2	2	
Arundinicola	6	3	1	2	
Pyrocephalus	6	2	2	2	+
Ochthornis	6	2	1	2	
Muscigralla	5	3	1	2	

TABLE II (continued)

Genus	I	II	III	IV	V
Satrapa	6	3	2	2	
Machetornis	6	2	2	2	
TYRANNINAE					
Muscivora	1	1	1	1	+
Tyrannus	1	1	1	1	+
Empidonomus	1	1	1	1	+
Legatus	2	1	1	1	
Sirystes	2	1	1	1	+
Myiodynastes	1	1	1	1	
Megarynchus	1	1	1	1	+
Corythotriccus	1	1	1	1	+
Myiozetetes	1	1	1	1	+
Tyrannopsis	1	1	1	1	+
Pitangus	1	1	1	1	+
Tolmarchus	1	1	1	1	+
MYIARCHINAE					
Myiarchus	2	1	1	1	+
Rhytipterna	2	1	1	1	+
Knipolegus	2	1	1	1	+
Mesotriccus	2	4?	1	3	
Muttallornis	6	1	2	1	
Contopus	6	1	3	2	+
Blacicus	6	1	3	2	
Empidonax	6	2	3	3	+

TABLE II (continued)

Genus	I	II	III	IV	V
Aschmolophus . .	6	2	3	2	
Cnemotriccus . .	6	2	2	2	
Mitrephanes . . .	6	2	3	2	
Terenotriccus . .	6?	2	3	3	
Myiobius	6	1	3	2	
Pyrrhomyias . . .	6	4?	3	2	
Myiophobus . . .	6	4?	2	2	
Onychorhynchus .	3	1	3	1	+
PLATYRINCHINAE					
Platyrinchus . .	3	4	3	3	
Cnipodectes . . .	1	4	1	2	+
Tolmomyias . . .	1	4	1	2	
Rhynchocyclus . .	1	4	2	2	
EUSCARTHMINAE					
Todirostrum . . .	2	4	2	3	
Oncostoma	1	4	1	3	
Euscarthmornis .	1?	4	1	3	
Lophotriccus . .	2	4	2	3	+
Colopteryx . . .	?	4	2	3	+
Myiornis	1	4	2	3	+
Poecilotriccus . .	3?	4	2	3	
Leptotriccus . .	?	4	2	3	
Phylloscartes . .	1	4	2	3	
Capsiempis . . .	2?	4	2	?	+

TABLE II (continued)

Genus	I	II	III	IV	V
Pseudocoloptenyx	2?	4	1	3	
Habrura	6	3	2	3	
SERPOPHAGINAE					
Tachuris	?	4	2	3	
Spizitornis . . .	5	4	2	3	
Stigmatura . . .	2	4	2	3	
Serpophaga . . .	5	4	2	3	
Inezia	5	4	2	2	+
Mecocerculus . .	5	4	1	3	
ELAENIINAE					
Myiopagis	1?	3	1	3	
Elaenia	5	1	1	2	+
Suiriri	5	2	2	2	
Sublegatus . . .	5	1	2	3	
Phaeomyias . . .	2	2	2	3	
Camptostoma . . .	2	4	2	3	
Xanthomyias . . .	1	4	?	3	
Tyrannisacus . . .	6	3	2	3	+
Tyrannulus . . .	2	3	?	3	
Microtricopus . .	2-3	4	1	3	
Lophotriccus . . .	3	4	1	2	+
Hemitriccus	5?	4	1	2	+
Pipromorpha . . .	5?	4	?	2	+

Plate VI, Figure 19. Sayornis "cinerascens," Pycraft, 1907, Figures 101c, 102b. Sayornis nigricans, Shufeldt, 1889, Plate V, Figure 18. Spizitornis parulus, Parker, 1875: 320-321; Plate LIX, Figures 4, 5.

Apart from the well-known variations in size and shape of bills, flycatcher skulls differ most in configuration of the cranium, palatines, and the interorbital and nasal septa. The principal types of the latter four characters are illustrated in Figures 2 and 3 and tabulated in Table II. The types of nasal septa, as well as other characters of the nasal region, will be further dealt with in a later section, as will the occurrence of palatomaxillaries.

The following generalizations apply to most species in the Fluvicolinae, Tyranninae, and Myiarchinae:

1. Straight prepalatines (Type 1) are associated with either broad or long bills. The prepalatines tend to converge anteriorly in forms with long, slender bills (e.g., Agriornis) and to be parallel in forms with longer, broad bills (e.g., Tyrannus, Gubernetes).

2. Sinuous palatines, either slender (Type 2) or expanded anteriorly (Type 3) are associated with either shorter, slender bills (e.g., Muscisaxicola, Type 2), or shorter, moderately broad bills (e.g., Empidonax, Type 2; Pyrocephalus, Type 3).

3. The Tyranninae and Myiarchinae, s.s. (Myiarchus through Fribates), are characterized by Type 1 crania,

palatines, and interorbital septa, and Types 1 or 2 nasal septa.

4. The Fluvicolinae and Myiarchinae, s.l. (Nuttallornis through Myiophobus), are characterized by Type 6 nasal septa and either Type 2 or 3 of at least two of the three remaining characters.

The remaining subfamilies do not lend themselves readily to characterization. The following points are worthy of note:

1. Tyrannus, Tolmarchus, Muscivora, Megarynchus, and Myiodynastes have unossified nasal capsules and incomplete maxillopalatines (Figure 6d). These genera are much alike in cranial features, differing specifically principally in shape and proportions of the bill.

2. Sirystes, Rhytipterna, Myiarchus, and Eribates are similar to the Tyrannus group, but have ossified nasal capsules and complete maxillopalatines (Figure 6d).

3. Legatus and Myiozetetes are less alike than the external appearance of the birds would lead one to believe.

4. Pitangus sulphuratus and P. lictor differ interspecifically to a degree greater than any other congeneric flycatchers examined. P. lictor has the most slender skull of any tyrannine examined.

5. Pyrocephalus and Savornis resemble more the Myiarchinae, s.l. (e.g., Contopus, Empidonax), than the Fluvicolinae.

6. Onychorhynchus is more like the Myiarchus section of the Myiarchinae than like the Contopus section, but most resembles Platyrinchus and Tolmomyias.

7. Nesotriccus appears intermediate in structure between the Myiarchinae (s.s.) and Todirostrum, but otherwise is probably more closely related to the former.

8. Elaenia and Myiopagis (united by some authors), on the basis of the species examined, appear to be distinct.

9. Fully ossified nasal capsules occur in the following genera: Legatus, Sirystes, Rhytipterna, Myiarchus, Eribates, Gubernetes, Colonia, Yetapa, Fluvicola, Ochthoeca, Myiobius, Myiophobus, Cnipodectes, Tyranniscus, Suiriri, Sublegatus, and Piprites, and in one individual each of Platyrinchus and Pyrocephalus. Evidence of ossification was found in partially damaged skulls of a few other genera of the smaller flycatchers.

10. Hellmayr's retention in the Tyrannidae of Stigmatura, Muscigralla, Habrura, Sirystes, Tyrannulus, and Microtriccus, transferred by Ridgway to other families on the basis of characters of the feet and legs (see discussion of Pipridae), appears to be justified.

B. Attilas (Cotingidae, Attilinae)

Genus included: Attila.

Attilas are like Tyranninae, differing as follows: interorbital septum less completely ossified (Type 5);

nasal septum incomplete (shallow) along entire length; prepalatines narrow, slightly convergent, nearly straight. Similar in over-all configuration to Agriornis and Xolmis.

C. Becards and Tityras (Cotingidae, Tityrinae)

Genera included: Pachyramphus, Platypsaris, Tityra, Erator (= T. inquisitor).

Illustrations: Tityra, Erator, Figure 7; Tityra (nasal capsule), Figure 8d.

Previous description and illustrations: Pachyramphus sp., Parker, 1875: 310-312; Plate LVII, Figures 4-7.

Pachyramphus, Platypsaris, and Erator are like the Tyranninae, differing as follows: interorbital septum less completely ossified in becards (Type 5); premaxillae above nares slightly swollen; nasal capsule ossified in Pachyramphus, partly ossified in Erator, and unossified in Platypsaris; prepalatines in Erator expanded at anterior end.

Tityra (s.s.) is like the becards, except premaxillae greatly swollen laterally; nasal capsule ossified, distorted (complete description under discussion of nasal region); interorbital septum ossified.

Maxillopalatines in tityras and becards recurved along posterior edge.

Type II Skulls

A. Manakins (Pipridae) and Cotingas (Cotingidae)

Genera included: (1) Pipra group (manakins). Antilophia, Corapipo, Machaeropterus, Manacus, Pipra, Teleonema, Xenopipo. (2) Cotinga group (cotingas). Carpodectes, Cotinga, Heliochera, Xipholena. (3) Euchlornis (berry-eaters). (4) Zaratornis. (5) Schiffornis.

Illustrations: Pipra mentalis (palate), Figure 4a; Cotinga cayana (palate), Figure 4b; Heliochera (nasal capsule), Figure 8b; Sapayoa aenigma (antorbital region), Figure 13.

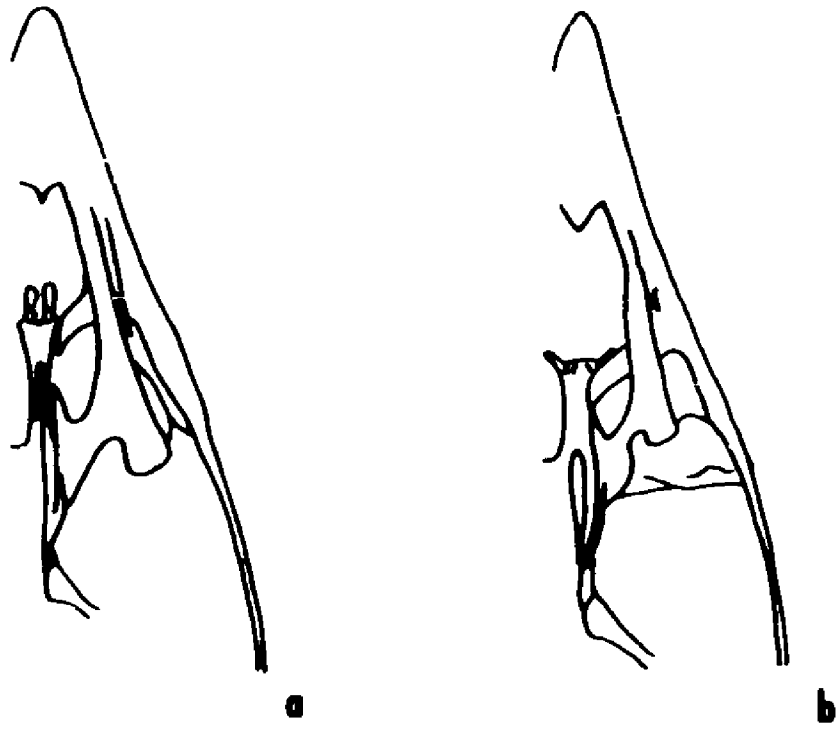
Previous description and illustrations: Pipra erythrocephala, Parker, 1875: 309-310; Plate XLII, Figures 1-3.

1, 2, 3. Pipra group, Cotinga group, Euchlornis

General description: Small to moderate skulls, 24-50 mm. Bill short, culmen slightly longer than orbit; broadly triangular, sides straight or slightly concave. Nares relatively large, with premaxillae anterior to prepalatines shorter than or equal to nares. Orbital roof variously flattened. Trend among manakins to depression and elongation of cranium; least evident in Pipra and Manacus. Quadratojugal arch bowed outward in Euchlornis and cotingas.

Interorbital septum largely unossified, both fenestrae extending full length of orbit, the upper one slightly

Figure 4. Type II and III Skulls. Palatal aspect. Type II: 4a, Pipra mentalis; 4b, Cotinga cayana. Type III: 4c, Querula purpurata; 4d, Cephalopterus ornatus.


a
b
c
d

longer. Superior and inferior fenestrae equal in height, except in least depressed forms (Pipra, Manacus, Euchlornis), in which case unequal, the lower being enlarged and the upper restricted in depth. Septum almost completely ossified in Cotinga group; lower fenestra small, circular, usually isolated from optic foramen by a thin strand of bone; upper fenestra also isolated, oval in shape, but obliterated in Heliochera.

Ectethmoids inflated (except in Euchlornis), with anterior surface more or less swollen, uniformly in the least inflated (Pipra, Heliochera) and bullate in the lower portion in the most inflated (Chiroxiphia, Xenopipo, Xipholena).

Lacrymals variable, usually more or less rotated to anterior surface of ectethmoid; expanded above and below, the lower portion (foot) often inflated to some extent and always resting on quadratojugal arch. Head variously compressed and elongated, failing to fit closely into frontonasal hinge (except in Manacus); medial end rotated downwards away from hinge and braced in most cases against maxillary process of nasal; shorter and not reaching nasal in Heliochera and Euchlornis.

Frontals broadly expanded dorsally over frontonasal hinge, more or less folded forward over hinge. Amount of folding greatest in cotinga skulls with flattest orbital roofs. Surface of frontals often more or less rugose,

with parallel longitudinal furrows sometimes extending back between orbits. Development of furrows variable among individuals, not present in all species.

Nasal capsule largely unossified, except in Heliochera. Base of nasal wall forming ridge ending at anterior edge of maxillopalatine in Euchlornis and Pipra group, extending onto dorsal surface of maxillopalatine in Cotinga group. Top of nasal septum ossified. Capsule ossified in Heliochera (amphirhinal), bulbous anteriorly; nasal septum, nasal and alinasal walls fully ossified; transverse oval plate within septum; alinasal and inferior turbinals fully ossified. Nasal septum in Teleonema with similar plate; septum fully ossified, nasal region otherwise unossified (holorhinal). Partial ossification of alinasal turbinals (posterior portion) in Euchlornis; posterior portion of capsule ossified in E. formosa.

Palatines: Pipra group--prepalatines moderate in width, converging and tapering anteriorly; broadest in Pipra and Manacus; interpalatine scrolls weak; transpalatines moderate, enlarged in Pipra and Manacus. Cotinga group--prepalatines tapering and convergent, shorter than in Pipra group; interpalatine plates sharply constricted laterally, elongated, directed more anteriorly to meet shortened prepalatines; mediopalatines each with a dorsal expansion articulating with base of ectethmoid (except in Heliochera); interpalatine spurs reduced,

scrolls absent; postpalatines elongated, somewhat flattened ventrally. Euchlornis--prepalatines intermediate in length between above groups; all elements of palatines narrower, narrowest in E. riefferii, with pre-, trans-, and interpalatines rodlike; mediopalatines without ectethmoid articulations.

Vomer narrow, flat, flared anteriorly. Maxillopalatine articular processes variously developed. Horns elevated medially in cotingas, except in Cotinga itself.

Pterygoid footplate variously elongated. Pterygopalatine joint inclined to a greater or lesser degree.

Maxillopalatines usually moderate in width, flat, blunt, recurved posteriorly to a greater or lesser extent at tip, overlapping ventral surface of vomer; usually twisted, higher behind, but sturdier in Cotinga group.

Palatomaxillaries present, well developed in manakins, Euchlornis, and Heliochera, but weak in Cotinga; not found in Carpodectes or Xipholena.

Summary of group differences: Cotinga skulls differ from manakin skulls in relative reduction in length of prepalatines, size of transpalatines, width of interpalatines, and size of interorbital fenestrae; greater inflation of ectethmoid plates, length of postpalatines, elevation of vomerine horns; possession of mediopalatine-ectethmoid articulations, slight bowing of quadratojugal arch, extension of base of nasal wall to middle of maxillopalatine.

Euchlornis differs from above groups in flatness of ectethmoids, intermediate length of prepalatines, and slenderness of palatine elements; manakinlike in interorbital septum and maxillopalatine contribution of nasal wall; cotingalike in quadratojugal arch.

4. Zaratornis

Zaratornis is like Cotinga group, differing as follows: Greater curvature of maxilla. Roof of orbits steep, no folding of frontals over frontonasal hinge. Interorbital width and antorbital complex (ectethmoid, lacrymal, frontal plates or "wings") reduced. Length of prepalatines greater, as in Euchlornis; trans- and postpalatines reduced in length; interpalatines broader and less angular.

Zaratornis is like Heliochera in having a more thoroughly ossified interorbital septum, well developed maxillopalatine-vomerine articulations, and large interpalatine scrolls. In all other characters mentioned above, Heliochera is intermediate between Zaratornis and other Cotinga type skulls.

Nasal capsule not ossified. Palatomaxillaries not found.

The Zaratornis type of skull is considered here to be derived from the Cotinga type through a further development of the divergent modifications exhibited by Heliochera.

5. Schiffornis

Schiffornis differs from the manakins as follows: Skull longer, more slender-billed; premaxillae anterior to nares slightly longer than nares. Palatines slightly longer; interpalatine scrolls more widely flared. Anterior end of vomer greatly expanded; horns widespread, joining widely separated ossified alinasal turbinals lying above prepalatine bars; nasal capsule otherwise unossified. Maxillopalatine articular processes of vomer large, hooking over anterior edge of maxillopalatines. Palatomaxillaries long, tending to fuse distally with prepalatine bars.

B. Bare-necked Grackles (Gymnoderinae)

Genus included: Gymnoderus.

Essentially a larger version (60-67 mm.) of the cotingine type of skull, differing from Cotinga group skulls as follows: Frontonasal hinge somewhat variable, tending to be raised above level of head of lacrymals laterally, but not medially; hinge sometimes a flat "V." Head of lacrymal hook-shaped. Frontals not folded over frontonasal hinge. Interpalatines not constricted; transpalatines short, slender. Vomer flat, as in Cotinga. Pterygoid footplate extremely elongate; pterygopalatine joint inclined to near-horizontal.

Palatomaxillaries short, slender, united partly or completely with maxillae.

Nasal capsule lightly ossified, broken out in most skulls; typically tyrannoid. Septum fully ossified with weak, slender, oval transverse plate at base.

C. Bellbirds

Genus included: Procnias.

Illustrations: Skull and palate, Figure 14.

Previous description and illustrations: Procnias nudicollis, Parker, 1875: 341-345; Plate LXII, Figures 5-8.

Moderately large skulls (57-63 mm.), with relatively short, weak, broadly triangular bills (narrowest in P. tricarunculata); premaxillae anterior to nares less than 3/4 length of nares. Over-all configuration of skull similar to skulls of Cotinginae, differing in greater depression of cranium (least in P. tricarunculata), compressed and ventrally bowed quadratojugal arches, and a number of extremely specialized modifications possibly derived as "exaggerations" of similar but weaker features of the cotingine skull. These modifications are discussed in detail in a later section (discussion of the larger fruit-eaters).

Type III Skulls

Fruitcrows, Pihas, and Umbrellabirds (Querulinae)

Genera included: Cephalopterus, Haematoderus, Lipaugus, Querula, Pyroderus.

Illustrations: Querula purpurata (palate), Figure 4c; Cephalopterus ornatus (palate), Figure 4d.

General description: Moderate to large skulls, 45-100 mm; corvine in general appearance. Bill (except in Lipaugus) long, about 1/2 total length of skull, sides straight or nearly so; premaxillae anterior to prepalatines 1 1/2-2 times length of nares.

A. Purple-throated Fruitcrows (Querula)

Moderate sized (55-57 mm) basic tyrannoid skulls, differing from the tyranno-myiarchine type as follows: Bill anterior to nares moderately swollen; interorbital septum ossified. Frontals above frontonasal hinge moderately flared dorsally and laterally, as wide as bill; head of lacrymal fitting closely into hinge. Ectethmoids swollen, upper and lower arms individually bullate anteriorly.

Nasal capsule unossified; septum long, completely ossified, extending posteriorly between vomerine horns. Anterior wall of nasal capsule incompletely joined to premaxillary border of nasal region, leaving a distinct aperture at the anterior margin of each naris.

Prepalatines slender, expanded anteriorly and posteriorly; transpalatines oblique. Interpalatine plates broad, processes (spurs) strong; scrolls broad, flat, widely flared. Postpalatines short. Mediopalatines

arched anteriorly and dorsally to meet base of swollen ectethmoid plates. Vomer broad, U-shaped in cross-section; horns flared and elevated medially; articular processes weak. Pterygopalatine joint with irregular moderately inclined suture.

Maxillopalatines moderately wide, parallel-sided, blunt, recurved dorsally along posterior margin. Palatomaxillaries absent.

B. Pihas (*Lipaugus*)

A shorter-, more slender-billed version of the *Querula* skull with bill slightly less than 1/2 total length of skull; premaxillae anterior to nares equal to length of nares. Lower ectethmoid bullae each with ventral bony boss, apparently articulating with upper surface of transpalatine. Vomer slenderer. Nasal capsule in *L. vociferus* and *L. cineraceus* nearly completely ossified.

C. Umbrellabirds (*Cephalopterus*) and Scutated Fruitcrows (*Pyroderus*)

Cephalopterus differs from *Querula* as follows: Large skulls (94-100 mm); bill narrower, premaxillae not swollen. Deep median cleft between arched frontal plates. Foot of lacrymal twisted anterolaterally, displaced by lower arm of ectethmoid that overlaps quadratojugal bar. Nasal capsule with anterior wall a transverse band of bone free of palatal surface below; precapsular aperture large.

Anterior ends of prepalatine bars each with abrupt broad medial expansion. Transpalatines and interpalatine plates broader, scrolls absent. Postpalatines long, flattened. Mediopalatine ectethmoid articular surface a broad, flattened plate. Maxillopalatines much broadened, arched above prepalatines, deflexed ventromedially.

Pyroderus similar to Cephalopterus, but smaller (82 mm). Frontal plates, trans- and interpalatines as in Querula. Lacrymals less inflated. Pterygoids broad, with unusually strong dorsal keel along entire length.

D. Crimson fruitcrows (Haematoderus)

Similar to Pyroderus in general conformation (79 mm), except premaxillae anterior to nares decurved. Frontal plates cleft, as in Cephalopterus. Palatines more like Querula, but entire complex longer, narrower, and more slender; prepalatine bars ribbonlike. Ectethmoids less inflated, not overlapping quadratojugal bar. Nasal capsule ossified, narrow and long, extending backwards to join reflexed rear margin of maxillopalatine via a bony bridge and forward to restrict precapsular aperture to a small foramen. Alinasal turbinals firmly united with broadened maxillopalatines that form a V-shaped brace into which vomer fits. Vomer narrow, crurae compressed; articulates with compound maxillopalatines, as in Rupicola.

Type IV Skulls

Cocks-of-the-rock (Rupicolidae)

Genus included: Rupicola.

Illustrations: Nasal capsule, Figures 7g, 8c; palate, Figures 10a, 10b.

Moderately large skulls (58-65 mm); bill strong, arched and compressed, nearly as long as cranium. Premaxillae anterior to nares 1/2 total length of bill in R. rupicola, shorter in R. peruviana. A unique type of skull, discussed in detail in a later section (discussion of the larger fruit-eaters).

Type V Skulls

Plantcutters (Phytotomidae)

Genus included: Phytotoma.

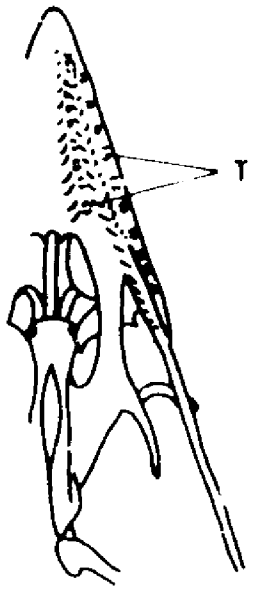
Illustrations: Palate, skull, mandible, Figures 5a-c.

Previous descriptions and illustrations: Phytotoma rara, Parker, 1878: 255; Plate XLVI, Figures 8-10. P. rara, Küchler, 1936.

Moderately small skulls (30 mm) fringilloid in appearance, with much decurved bill. Orbital roof flattened, sharply decurved anteriorly. Temporal fossae large, flat, with postorbital processes (above) absent and zygomatic processes (below) greatly enlarged. Parasphenoidal rostrum broad, with interorbital septum above fully ossified and thick.

Ectethmoid plates flat, angled forward when viewed

Figure 5. Type V and VI Skulls. Type V: a-c, palate, skull, and mandible (left 1/2, dorsal) of Phytotoma rutila. Type VI: d-f, palate, skull, and mandible (left 1/2, dorsal) of Oxyruncus cristatus. Symbols: C, cartilaginous nasal floor; I, internal process; R, retroarticular process; T, tubercle.



a

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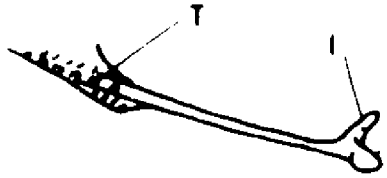

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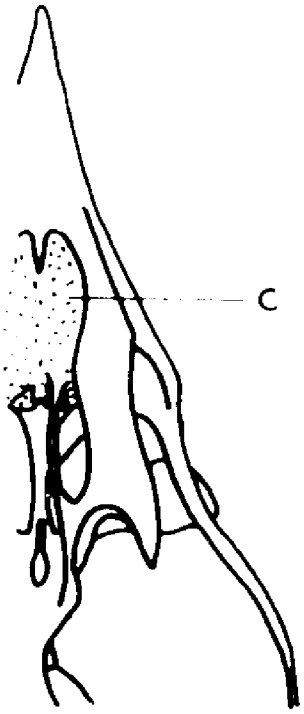


d

e

f

from above; widest below level of raised frontonasal hinge; lower arm of each elongate, braced against quadratojugal bar. Lacrymals greatly reduced, each present as adherent splint on edge of ectethmoid. Distinct elongate depression along top of orbital margin of frontals (attributed by Parker to enlarged nasal glands).

Premaxillae each with double row of low tubercles on palatal surface. Nasal capsule ossified; anterior end floored by premaxillae, restricting "palatal vacuity." Nasal septum ossified, inflated above vomer. Vomer short, broad, decurved, U-shaped in cross-section; horns high, embracing nasal septum on either side, decurved to articulate from above with inflated alinasal turbinals. Maxillopalatines recurved along posterior margin; fused posteriorly to alinasal wall; anterior portions flooring nasal capsule behind.

Palatines arched (twisted) behind. Prepalatines short, broad; transpalatines long spurs. Interpalatines broad, angled forwards; interpalatine processes (spurs) short; scrolls produced ventrally as vertical plates.

Mandible with anterior 1/3 tuberculate above, decurved, depressed, and with expanded lateral flanges, diamond-shaped when viewed from above; flanges grooved above for reception of tomia of upper bill. Rami compressed, high behind. Retroarticular processes reduced; internal processes enlarged, recurved posteriorly, each

ramus appearing tipped by a large "V," open behind.

Type VI Skulls

Sharpbills (Oxyruncidae)

Genus included: Oxyruncus.

Illustrations: Palate, skull, mandible, Figures 5d-f.

Skull icteroid in conformation (39 mm). Bill slender, abruptly deflexed. Quadratojugal bars constricted at level of lacrymals. Cranium flattened, supraorbital depressions present, as in Phytotoma. Frontal plates broadly rounded; frontonasal hinge high, above level of lacrymals. Lacrymals normally tyrannoid. Ectethmoids slightly inflated, contacting palatines below. Interorbital septum ossified.

Maxillopalatines flattened, slightly deflexed. Palatines (prepalatines and interpalatines below ectethmoids) broad, U-shaped along entire length; prepalatines united laterally to palatal surface of bill for 1/2 their total length, angled medially from point of union.

Nasal capsule floored by heavy cartilaginous sheet (united posteriorly with vomer) from which arise strong tendinous (?) bands passing posteriorly to join each interpalatine process (spur). Anterior 1/2 nasal septum ossified. Transpalatines long, slenderer than prepalatines. Interpalatine scrolls flared. Palatomaxillaries absent.

Mandible with retroarticular processes long.

PROMISING TAXONOMIC CHARACTERS

The Nasal Region

The tyrannoid nasal capsule, insofar as can be determined from skulls, appears to be relatively constant in its major morphological features. Any marked departure from such a typically conservative feature merits attention, since it may be of systematic importance. As the nasal capsule in most birds is essentially an unossified organ, a definitive study would require extensive histological and developmental investigations. These I have not had the opportunity to do. However, among the Tyrannoidea, various elements of the cartilaginous capsule often become ossified and can be studied in prepared skulls.

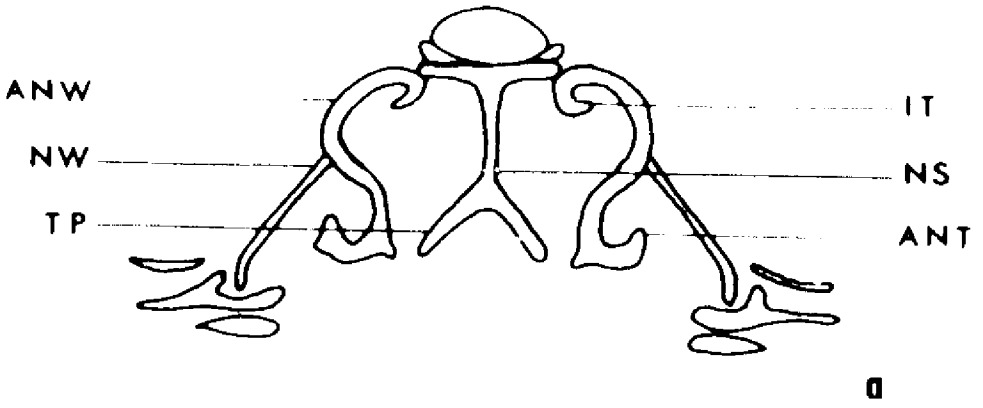
The development of the nasal capsule has been studied in a number of nonpasserine birds by several investigators. The passerine nasal capsule was investigated by W. K. Parker nearly a century ago. His opinion was that it would prove to be a character of considerable systematic value, yet it appears to have received little attention since his time. As this discussion is based largely on Parker's (1875) analysis of the passerine nasal capsule in Corvus, his original terminology will be used. Subsequent works have been summarized by de Beer (1937), together

with a synonymy of later terms.

Within the nasal capsule there arise three pairs of cartilaginous turbinals. Anteriormost are the alinasal turbinals, often visible through the external nares. They extend posteroventrally to articulate with the anterior end of the vomer. Dorsal and slightly medial to the alinasal turbinals lie the inferior turbinals, which extend posteriorly toward the ectethmoid walls. Dorsal and posterior to the inferior turbinals, against the ectethmoid walls, lie the upper, or superior, turbinals.

Among the group of birds under consideration here, there is often seen a pair of small bones, separated by the nasal septum, that lie between the prepalatine bars and join the horns of the bicornuate vomer (Figure 6c). These are the alinasal turbinals, ossifications of the cartilages of the same name. In a number of cases each is joined to an ossified alinasal wall that passes posteroventrally along the top of the ossified nasal wall to join with the maxillopalatine. The base of the alinasal wall may pass inward at this point, toward the vomer, as an inturned alinasal lamina. The alinasal wall itself continues posteriorly, passing beneath the maxillary process of the nasal bone (Figure 6b). The condition thus formed, with two external openings--the naris itself and the passage beneath the maxillary process of the nasal--is known as amphirhiny. The base of the nasal wall may ossify and

Figure 6. The Tyrannoid Nasal Region. Figure 6a, cross-section of nasal capsule of Corvus (from Parker, 1875); b, c, Myiarchus; d, Myiarchus (left half) and Tyrannus (right half). Symbols: ANW, alinasal wall; ANT, alinasal turbinal; IT, inferior turbinal; MXP, maxillopalatine; NF, nasal floor; NS, nasal septum; NW, nasal wall; TP, transverse plate (trabeculum); V, vomer.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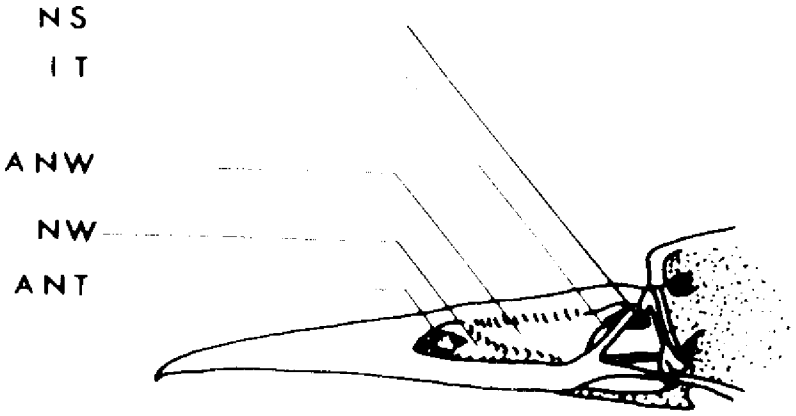
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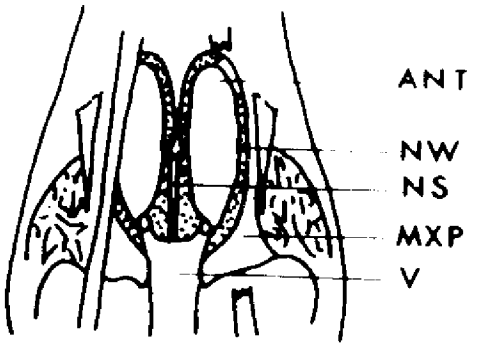
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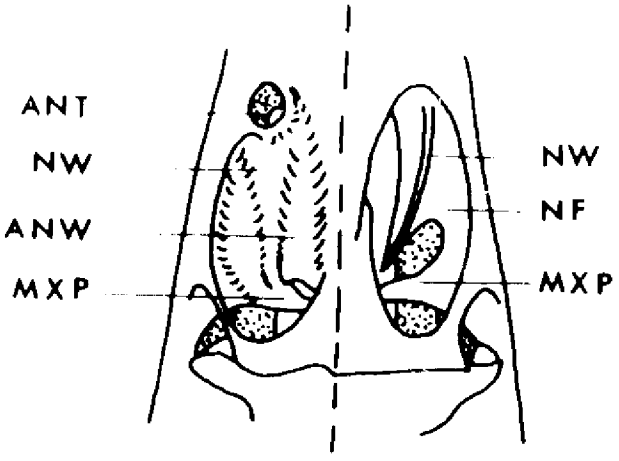

ANT
NW
ANW
MXP
NW
NF
MXP

d

contribute to a broadened maxillopalatine. Typically, however, the wall of the nasal capsule is unossified.

There is frequently encountered along the base of an ossified nasal septum, where such occurs, a transverse trabecular plate (Figures 6a, 8b, 8c, 9), an ossification of the cartilaginous "nasal trabeculum." Ventral to the anterior end of the trabecular plate there is often a small median triangular projection from the fused premaxillae (Figure 9); it represents an ossification of a recurrent alinasal lamina from the anterior wall of the nasal capsule. In some cases the recurrent lamina is covered by, or incorporated into, a partial flooring of the nasal capsule formed by a posterior extension of the premaxillae into the anterior portion of the vacuity between the prepalatine bars (Figure 1a).

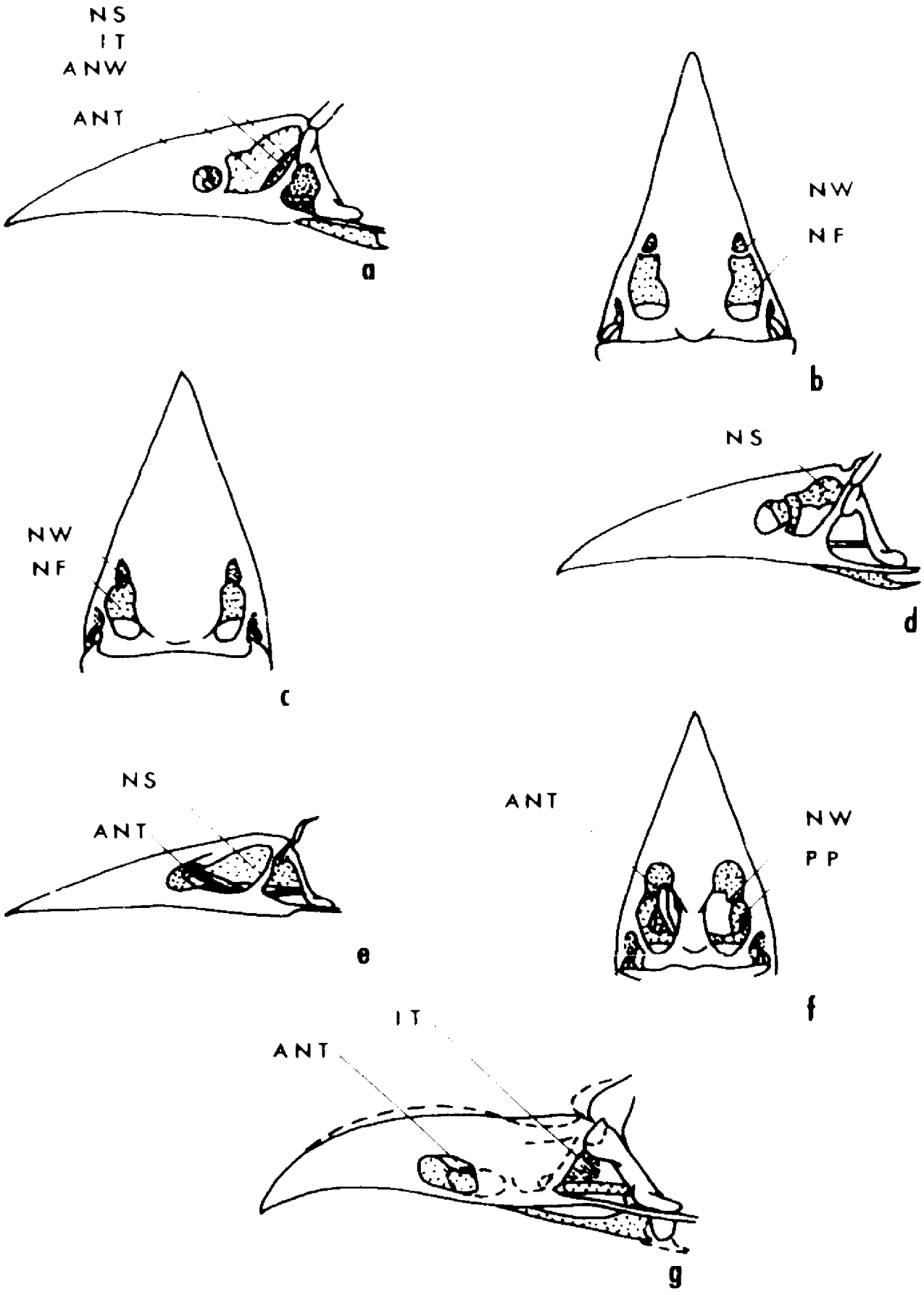
Figure 6 illustrates, in addition to Parker's cross-section of the cartilaginous capsule of Corvus, the lateral and ventral aspects of the ossified capsule in Myiarchus, and unilateral dorsal views of the nasal region in Myiarchus and Tyrannus. The Myiarchus capsule represents a nearly complete ossification of the condition fairly typical of skulls of most tyrannoid genera examined with the exceptions of Rupicola and Tityra. Such extreme ossification results in the typical amphirhinal skull in which there are two external openings in the bill. Tyrannus represents the least ossified, or holorhinal,

condition, in which there is but a single, large opening.

As can be seen in the cross-section (Figure 6a), the nasal region is divided by a median nasal septum that is based by a transverse, deflexed, trabecular plate. It is bounded laterally by the alinasal and nasal walls. The alinasal wall passes inwards to form two of the three pairs of turbinals that may be found ossified. These are the alinasal and inferior turbinals. A third pair, the upper, or superior turbinals abut the anterior wall of the orbit but rarely ossify in these skulls. In the event of the failure of the wall of the nasal capsule to ossify, as in the holorhinal Tyrannus skull, the base of the nasal wall is usually found ossified along the nasal floor (Figure 6d, left half). It extends obliquely backward to join the maxillopalatine. Tyrannus is an exception in that the completeness of this union varies individually among the species. The least complete condition is figured (Figure 6d, left half). The alinasal turbinals often ossify in holorhinal skulls but are usually lost in preparation, since there are no ossified capsular walls to which they may join.

Figure 7 illustrates the principal variants from the basic tyrannoid pattern illustrated in Figure 6. Among the genera Tityra (s.l.) and Rupicola there are constant specific differences, in contrast to the uniformity within genera and groups of genera among the other members of

Figure 7. Principle Variants of the Typical Tyrannoid Nasal Capsule. Figure 7a and b, *Tityra semifasciata*; c and d, *T. cayana*; e and f, *T. inquisitor* (= *Erator*); g, *Rupicola peruviana* (solid line) and *R. rupicola* (broken line). Symbols as in Figure 6.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the superfamily.

Tityra semifasciata (Figures 7a, 7b) exhibits what might be termed a fully ossified nasal capsule, having almost as great a degree of ossification as is encountered anywhere among the Tyrannoidea. The nasal capsule of T. cayana (Figures 7c, 7d) is similar, but less thoroughly ossified. The nasal region of immature specimens of semifasciata resembles that of the adults of cayana. The nasal capsule of Tityra inquisitor (Figures 7e, 7f), a species sometimes set aside in the genus Erator, is the most different of the three, and it is also the least ossified. These three species seem to form a series of increasing specialization from T. inquisitor through cayana to semifasciata.

In T. inquisitor only the septum, alinasal turbinal, and the base of the alinasal wall are ossified. The naris is constricted above and below, and the nasal wall is transverse, rather than oblique. In T. cayana the constriction of the naris is greater and the transverse nasal wall is correspondingly higher. The nasal wall passes backward at right angles to its lateral protrusion at the level of the naris to join the maxillopalatine but this is obscured in the illustration by the swollen condition of the bill above it. The nasal floor is ossified.

Adult T. semifasciata show a nearly complete ossification of the nasal capsule. The naris is completely

isolated by the ossified nasal wall. The alinasal turbinal is much reduced when contrasted with that of inquisitor.

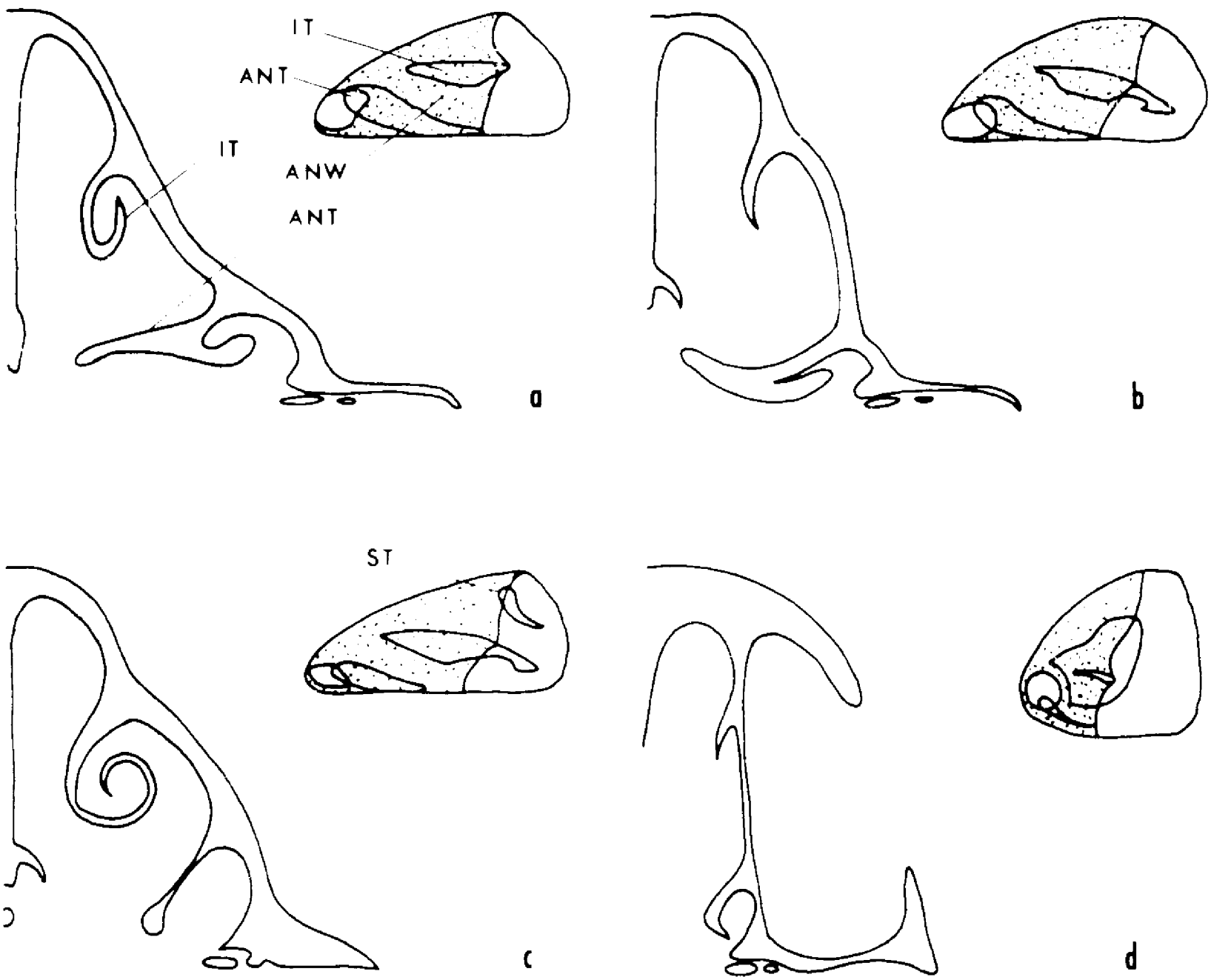
In general configuration of the bill T. semifasciata and cayana depart significantly from the more nearly typical tyrannoid configuration of inquisitor.

The cocks-of-the-rock also differ specifically, as well as generically, from the tyrannoid norm (Figure 7g). Rupicola peruviana is unique in that the surface of the bill ossifies immediately over the nasal walls, enclosing the capsule in a double bony wall. It is thus secondarily holorhinal. R. rupicola is amphirhinal. Other interspecific differences will be enumerated in a later section.

Figure 8 illustrates diagrammatic cross-sections and lateral views of the fully ossified capsules of the three principal tyrannoid types. Heliochera is a fairly typical cotinga and is included for purposes of comparison with the other forms. The cross-sections represent one-half the nasal region as reconstructed from unsectioned skulls. They are not strictly vertical sections in that slight adjustments have been made in order that most major features could be shown in each. The capsular walls in the lateral views are rendered as dotted screens so that the turbinals within are visible. The septum is not shown in the lateral views.

The capsules of Myiarchus and Heliochera (Figures 8a,

Figure 8. Reconstructions of Tyrannoid Nasal Capsules. Explanation in text. Figure 8a, Myiarchus; b, Heliochera; c, Rupicola peruviana; d, Tityra semifasciata. Symbols: ANW, alinasal wall; AT, alinasal turbinal; IT, inferior turbinal; ST, superior turbinal.


IT
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8b) are typically tyrannoid and are essentially similar in their major features, although that of Heliochera is relatively compressed at the base. This compression is in reality due to a heightening of the bill as well as a broadening of the premaxillae outside the nasal capsule. The septum is accordingly shallower. The trabecular plate is present and occurs within the septum. The inferior turbinal is less coiled, but produced to the rear beyond the alinasal wall.

The capsule of Rupicola peruviana is less compressed than that of most cotingas. It is unique among the Tyrannoidea in that the dominance of the alinasal turbinal over the inferior turbinal above it are reversed, with the alinasal turbinal much reduced. The third, or upper turbinal is ossified. In R. rupicola the two larger turbinals are nearly equal in size.

In the case of Tityra semifasciata (Figure 8d), the entire nasal capsule is proportionately reduced in length by a heightening of the bill. The premaxillae are expanded above and below to such an extent that the entire capsule has been enclosed within a ring of bone above its surface. The turbinals are considerably reduced, as is the area encompassed by the walls of the capsule itself. There is no trabecular plate associated with the septum.

The least consistent feature of the tyrannoid nasal region, and possibly one of the greatest over-all taxonomic

importance, is the nasal septum and its associated internal supporting structures.

The nasal septum is invariably ossified in skulls with ossified nasal capsules but it may also ossify independently. Table III enumerates representative genera in which ossified nasal septa occur (for types of septa, see Figure 2). Types 1 and 2 lack the transverse plate; Type 1 lacks internal support, and Type 2 contains a nearly vertical rod. Type 3 is like 2 except the internal rod is swollen and expanded laterally. Types 4, 5, and 6 possess the transverse plate. In Types 4 and 5 the plate is within the septum, oblique in 4 and more horizontal in 5. The plate in Type 6 is horizontal or nearly so and bases the septum.

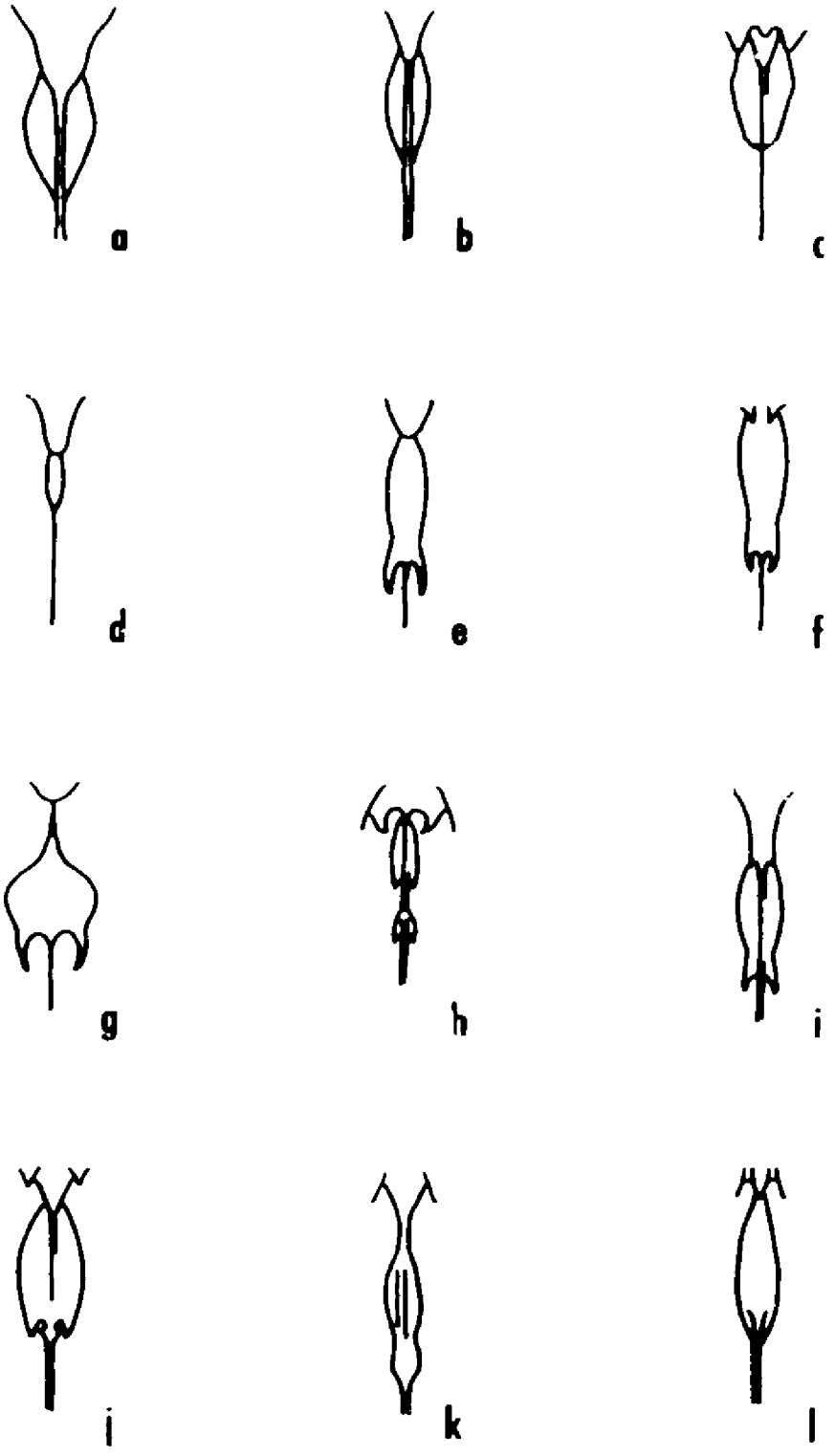
The transverse plate is variable in shape (Figure 9) and, combined with the above Types, seems to be a promising taxonomic character. In the Rupicolidae, Pipridae, and Cotinginae (Figures 9a, 9b, 9c), it is oval and is located within the septum (Type 4, Pipridae; 5, Rupicolidae and Cotinginae). In Tyrannidae it is usually forked posteriorly, basing the septum (Type 6).

In the tyranno-myiarchine skulls (see Table II and later discussion on Tyrannidae) the plate is absent. Septum Types 1 and 2 occur in Tyranninae and Type 2 in Myiarchinae, s.s. Type 6 occurs in Myiarchinae, s.l. and in Fluvicolinae. In the Fluvicolinae the plate has a

TABLE III. Types of Nasal Septa in Representative Genera. Column I, type of nasal septum. Column II, genera with ossified nasal septum only. Column III, genera with completely ossified nasal capsule, including nasal septum.

Taxon	Genus	I	II	III
Pipridae	Teleonema	4	+	
Cotinginae	Heliochera	5		+
Gymnoderinae	Gymnoderus	6	+	
Querulinae	Querula	1	+	
	Haematoderus	1		+
Tityrinae	Tityra	2	+	
	Erator	2	+	
	Platypsaris	2	+	
Tyranninae	Tyrannus	1	+	
	Legatus	2		+
Myiarchinae	Myiarchus	2		+
	Contopus	6	+	
	Onychorhynchus	3	+	
Fluvicolinae	Agriornis	6	+	
	Gubernetes	6		+
Platyrinchinae	Platyrinchus	3		+
	Rhynchocyclus	3	+	

Figure 9. Representative Nasal Trabeculae. Figure 9a, Rupicola peruviana; b, Teleonema filicauda; c, Heliochera rubrocristata; d, Gymnoderus foetidus; e, Xolmis irupero; f, Empidonax flaviventris; g, Colonia colonus; h, Elaenia obscura; i, Serpophaga subcristata; j, Sublegatus modestus; k, Inezia subflava; l, Tchitrea nigriceps (Muscicapidae).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long, broad fork (Figure 9e), as opposed to the Myiarchinae, s.l., in which the plate has a short, narrow fork (Figure 9f). The Platyrinchinae and Onychorhynchus have a Type 3 septum. Among the remaining three subfamilies of smaller flycatchers a variety of septal types occur (Table II). Since the skulls of the latter birds are small and lightly ossified, many are damaged, and the nature of the septum cannot be adequately ascertained for many species.

In view of the correlation of the features of the nasal region (in the species in which these are ossified) with other morphological features, the nasal region seems to hold the promise of becoming a prime taxonomic character, as predicted by Parker nearly a century ago. In order to ascertain the true value of these features as indicators of relationships, a study must be made of the unossified cartilaginous structures of the nasal region. If it can be shown that the indications provided by the sporadically occurring ossifications of the nasal region found in this study are representative of basic trends, the nasal region may provide a primary taxonomic character complex useful within the Tyrannoidea.

The Palatine Process of the Premaxilla (Palatomaxillary)

The palatomaxillaries in passerine birds have received the attention of Amadon (1950), Tordoff (1954), Jollie

(1958), and Bock (1960). Neither Amadon nor Bock were able to discern any taxonomic significance in the form or occurrence of the processes, but Tordoff found it a useful character in the nine-primaried oscines. Tordoff's conclusions were supported by opinions of Mayr (1955) and Stresemann (1959).

The palatomaxillary is considered by Jollie and Bock to represent the embryonic palatine process of the premaxilla. The absence of the process is taken by most authors as evidence of fusion with the prepalatine bar, although Amadon was of the opinion that such a viewpoint might constitute an unwarranted generalization.

Bock has performed a task of considerable magnitude in his survey of the palatine process of the premaxilla in passerine birds (Bock, op. cit.). All of the material used by him was in the collections of the American Museum of Natural History and the United States National Museum. I have been able to examine all of the tyrannoid material in the National Museum and skeletons of those genera from the American Museum that were not represented in the National Museum. There are a number of discrepancies among our observations on the skulls of the suboscine material from the same collections. Unless otherwise noted, the examples used in the following discussion are presumably the same skulls examined by, or at least available to Bock.

Cotingidae: Bock recorded the process absent in Ampelion (2 specimens), Calyptura (1), Cephalopterus (3), Cotinga (1), Gymnoderus (1), Lipaugus (1), Procnias (7), Rupicola (5), and Tityra (3). He found it in four specimens of Euchlornis and 2 or 3 specimens of Pachyramphus.

Two specimens of Ampelion rubrocristata (= Heliochera) both have the process. In one (AMNH 6141) the process on one side is as described by Bock for Euchlornis; the other appears to have been broken off at the base. The second (AMNH 6142) has some lightly keratinized tissue over the surface of the palate, but under suitable magnification and illumination the processes can be seen lying adjacent to the prepalatine bars; at first sight they appear "fused," but on closer examination clear lines of demarcation can be seen.

Cotinga (USNM 321618) has two processes that are very short but are otherwise not significantly different from those in Euchlornis and the manakins, all of which possess well developed palatine processes free for a greater portion of their length along the medial (prepalatine) surface.

Rupicola is unique in the degree of lateral placement of the free prepalatine process. In R. rupicola the process is free in all six USNM specimens examined and extends posteriorly along the maxilla almost to the quadratojugal bar. Although developmental investigations are

necessarily beyond the scope of a survey of this nature, a skull of an immature R. peruviana (USNM 428779, exact age unknown) has been most instructive (Figure 10a). That the prepalatine process of the premaxilla is associated along its entire length with the maxilla can be clearly seen. Ossification of the palatal surface proceeds posteriorly incorporating the prepalatine bar as far as, or slightly beyond the anterior end of the nasal capsule. The prepalatine process of the premaxilla is visible in the adult skull as an elongate, raised, triangular area, free of the maxilla only at its distal end (Figure 10b). The free portion is less developed in R. peruviana than in R. rupicola. In 7 of 10 adult skulls in the USNM collection the process is readily apparent.

A raised area, similar to that in Rupicola but broader, is evident in skulls of Procnias. This elevation is labeled "p. px." (prepalatine process of the premaxilla) in Parker's figure of P. nudicollis (Parker, 1875, Plate LXII, Figure 8), and is evidently the same as that in Rupicola, except that there is no free end. Each of 2 specimens of P. alba (USNM 345689, 346343) has a short free process at the end of each of these triangular areas, as in Cotinga.

A specimen of Gymnoderus obtained from the University of Michigan collections (UMMZ 208556) with some of the palatal membranes intact had what appeared to be two small but well formed free processes arising basally from the

Figure 10. Palatine Process of the Premaxilla.

a. Rupicola peruviana, immature. USNM 428779.

b. Rupicola peruviana, adult. USNM 428736.

c. Gymnoderus foetidus. From UMMZ 208556.

Process fused to maxilla.

d. Querula purpurata. From USNM 428840.

Process fused to maxilla.

e. Tityra semifasciata. LSUMZ 22707.

Process with basal "suture."

f. Tityra inquisitor. LSUMZ 32051.

Drawn from right side; left process short, with attached tendon.

g. Tyrannus tyrannus.

Process short, no suture (compare Myiarchus, Figure 6c).

h. Tyrannus tyrannus.

Process short, "suture" present.

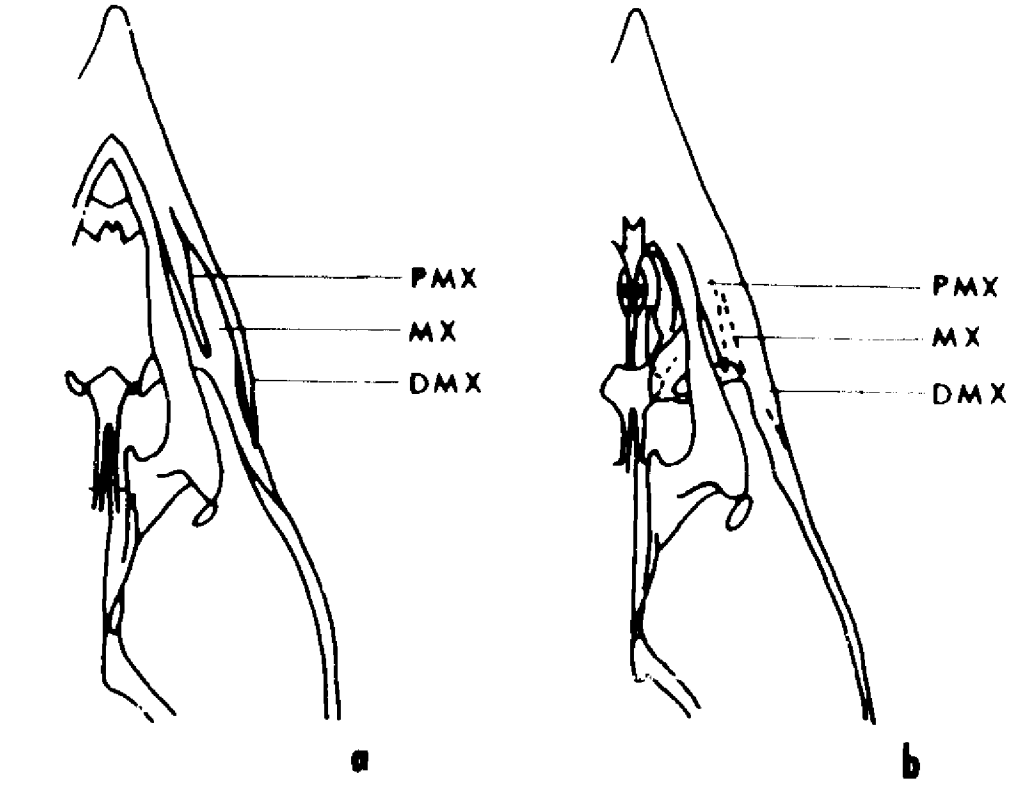
i. Tyrannus tyrannus.

Process long, with "suture."

j. Sayornis phoebe. From USNM 427803. Redrawn after sketch.

Process short, with "suture."

Symbols: DMX, dentary process of premaxilla; MX, maxilla; PMX, palatine process of premaxilla.


PMX
MX
DMX
PMX
MX
DMX
a
b
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j

anterior ends of the palatines. Removal of tissues on one side disclosed a high ridge bonded laterally along its entire length to the maxilla (Figure 10c). Two specimens (USNM 346063, 346064) show similar ridges with truncate tips incompletely joined to the maxilla. A fourth specimen (UMMZ 208517) has the premaxilla produced ventromedially as a flange along the maxilla.

Skulls of Querulinae (Cephalopterus, Haematoderus, Lipaugus, Pyroderus, and Querula) exhibit indications of a short, broad, triangular "plateau" on the palatal surface of each maxilla, joined to the palatine by a flange extending to the base of the prepalatine bar.

Seventeen specimens of three species of Tityra in the USNM all have free processes (Figures 10e, 10f). These processes are similar to those found among the Tyrannidae (see below). The becards (Pachyramphus and Platypsaris), attilas (Attila), and mourners (Rhytipterna) also have flycatcherlike processes.

Pipridae: The skulls of manakins, all of which have free processes, in many cases show a triangular ridge leading to, and continuous with each free process. The processes in Tyranneutes appears flycatcherlike.

Tyrannidae: A free palatine process is found in the skulls of many genera. Bock reported it present in 20 genera. Based on all material examined, I have found it in a total of 37 (see Table II). As larger series of

skulls are accumulated for genera in which it has not yet been found, it may be recorded for many more.

The process is variable both in place and in degree of attachment, as well as in length (Figures 10g-j). This variation may occur within long series of a single species (where these are available) as well as among species and genera. The free process may lie close alongside the palatine or arise more laterally from the general surface of the premaxilla, but in all cases seems associated with the latter bone. It may arise adjacent to the tip of the prepalatine bar or more posteriorly, even as far as the base of the maxillopalatine. It may be fused solidly at its base with the premaxilla, but more commonly is separated from that bone by an oblique basal "suture." The process in its usual form can be easily detached, and may or may not leave a visible scar. As a result it may be lost in preparation, cleaning, or careless handling. In those species in which it normally occurs, its absence, either unilaterally or bilaterally, is not accompanied by any expansion of the prepalatine bar to indicate fusion with that bone. Conversely, presence of the process in individuals of species that normally lack it, and in which the anterior end of the prepalatine bar is normally broadened, is not accompanied by a narrowing of the expanded portion of the latter bone to indicate any separation from it. The process is often accompanied by a

raised triangular area leading into the free process that may or may not possess a visible "suture."

Two series of adult Tyrannus (15 T. tyrannus and 16 T. dominicensis, each at least one year from fledgling, as determined by the attenuation of the primary flight feathers) were prepared. After recovery from the beetle colony these skulls were not further cleaned by boiling, bleaching, or soaking. Remaining tissues, if any, were carefully dissected away. One or both processes were found in all but two especially clean skulls (this method probably should not be relied upon to demonstrate the process in very small skulls, since the processes are very fragile and offer little resistence either to beetle jaws or forceps). The processes are often closely adherent to the overlying membranes in the dried skull and aften come away with the tissue being removed.

In a few skulls of the above series the process lay so close to the palatine that it appeared that it might be fused to it. In such skulls, with the overlying membranes intact, the process could be gently depressed with a probe and be seen to move freely. I found that this operation, when performed on skulls lacking the membranes, could result in loss of the process.

An occasional skull was encountered in the course of this survey that seemed to have one or both of the processes partly fused to the palatine at the distal end.

Rather than risk damage to museum material of this nature, I did not pursue the point. If such a fusion actually does occur among the flycatchers it is probably abnormal, and does not necessarily represent a primary developmental pattern.

Developmental stages of passerine skulls examined by Parker (1872, 1873a, 1873b, 1875), Jollie (1958), and Bock (1960) apparently did not include any suboscine material. Figures of immature oscine skulls in the latter two papers show the developing prepalatine process of the premaxilla to be unassociated with the developing maxilla in the way that it is in Rupicola. As such, Bock's generalization that the absence of the prepalatine process of the premaxilla in the adult skull is evidence of fusion with the prepalatine bar may be valid for the oscines. Based on the evidence present here it seems that the extension of that generalization to the suboscines (at least to the tyrannoid assemblage) may have been premature, especially since Bock himself recognized the possibility of fusion with the maxilla in Cotinga and Cnipodectes.

The evidence presented here is largely circumstantial, but perhaps no less so than that which exists for the bulk of the oscines. It is possible that among the Tyrannoidea the palatine process fuses basally to the palatine as well as to the maxilla, and that this fusion is obscured by the extensive anterior palatal ossification that occurs in many

species. The great variation exhibited suggests the possibility that the type of process found among the Tyrannidae may not be a homolog of the embryonic prepalatine process but merely an ossified tendon. Only developmental investigations can provide the necessary information on which to base accurate interpretations.

A developmental investigation of the skull of Tityra inquisitor (= Erator) is needed. T. inquisitor (Figure 10f) has both an anteriorly expanded prepalatine bar and a free prepalatine process (palatomaxillary), which may be an ossified tendon. A few skulls of Tityra (s.s.) and Platypsaris show a tendency towards fusion of the free process at its distal end with the prepalatine bar. Complete fusion of the process would render the prepalatine bar similar in configuration to that of Querula. Skulls of Querula, T. inquisitor, and the becards are otherwise at least superficially similar in general conformation to many flycatcher skulls. Should the palatomaxillary of T. inquisitor and the relatively ill-defined raised triangular area on the maxillary surface of the Querula skull prove not homologous with the embryonic prepalatine process of the premaxilla, the mere presence or absence of an ossified tendinous process would not carry as great a phylogenetic significance as would a more fundamental difference in development. There would then be only relatively minor differences separating Querula, T. inquisitor, the becards,

and many of the flycatchers. Thus it may be that the homologies of the free process in T. inquisitor and of the processes in the attilas, becards, flycatchers, and other tityras on the one hand, and Querula, the larger fruit-crows, bare-necked grackles, cotingas, manakins, bellbirds, and cocks-of-the-rock on the other, may provide a significant clue to the basic relationships of the birds themselves.

DISCUSSION

General Considerations

Biologists are constantly in search of "nonadaptive" characters to use as indicators of phylogenetic relationships, yet the skull, precisely as a result of its adaptation as a feeding mechanism, has proven a most useful tool in tracing the evolutionary changes that have taken place in many vertebrate groups. The avian skull, probably as a result of its highly specialized kinetic nature, has a relatively high level of adaptability at relatively low taxonomic levels. This adaptability has best been demonstrated among diverse forms of relatively closely related birds such as the Hawaiian Honeycreepers (Drepaniidae) and the Galapagos Finches (Geospizinae). One must bear in mind, however, that continental situations in which there are many groups of birds present would not provide a wide array of niches available to only one "ancestral stock" without there being simultaneous competition from other stocks for those same niches.

The ancestral stocks of the present day drepaniids and geospizines probably arrived at their respective island homes to find few, if any, other birds present in the feeding niches that their descendants presently occupy.

Such opportunities for adaptive radiation would be fewer in a continental situation with more potential competitors present. More weight can be accorded the skull as an indicator of relationships in a continental than an insular situation.

Since organisms are exposed to selective forces in the environment as integrated units, and the radiation of related forms, within the limits of genetic potential, is restricted only by the availability of niches, the uniform evolution of a single character or character complex to the exclusion of changes in other characters is unlikely, if not impossible. The same character may evolve at different rates when compared with other characters. Then, too, organisms may evolve functionally similar modifications in different ways (see Bock, 1959), regardless of their degree of relationship.

The very complexity of relationships among organisms and their environment would seem to preclude automatically the use of any single character as an <u>absolute</u> indicator of relationships among a broad spectrum of related forms. Such a character might well apply to a large number of species within a given group but not necessarily to all.

The point must be made that the relative importance of adaptive modifications of single characters as indicators of phylogenetic relationship varies inversely with descent through the hierarchy of taxonomic categories (downwards to

species). Character complexes are of relatively greater importance at higher levels than any of the single characters that compose them. Each case, of course, must be weighed on its own merits.

Such a limitation as that inherent in the use of a single adaptive character may apply to a so-called "non-adaptive" character as well, should such, in fact, exist. Variation within the limits at which selective forces might be brought to bear undoubtedly occurs. The tarsal envelope in the Tyrannoidea seems to be an excellent example.

Bock (1964) gives an excellent summary of the bird skull as a working unit. That anyone who accepts the current tenets of evolution should doubt the adaptive nature of the avian skull as a wholly integrated feeding unit does not seem likely. Use of the skull as an indicator of phylogenetic relationships must accordingly be judicious.

In spite of the demonstrated evolutionary plasticity of the bird skull (Simonetta, 1960; Bowman, 1961; and others), there is, among the birds examined in this survey, a remarkable correspondence of the major morphological groups of skulls with similarities in plumage and general conformation and, so far as is known, in behavior and other, internal morphological features seemingly unrelated directly to feeding habits.

The strict application among the Tyrannoidea of

characters of the feet and legs that have been used to place in separate families or subfamilies certain species that appear otherwise closely related seems to me to create artificial isomorphs where, in fact, homeomorphs probably exist. Conversely, to unite seemingly dissimilar species using the same apparently superficial characters seems equally inexpressive of natural relationships. I make no claim that in all cases tyrannoid skulls are indicative of relationships. Similarly, characters of the feet and legs are undoubtedly useful in many cases but certainly not in all. For isomorphism to exist in a simple structure like the tarsal envelope is far more likely than in a unit so complex as the skull. As so aptly expressed by Garrod (1877a: 450), ". . . the probability that the same complex conformation should appear de novo varies inversely as the complexity: the greater the elaborateness the less the chance that it, in all its detail, comes into existence more than once."

Relative to other, noncranial characters the systematic value of differences among similar skulls in similar birds are more easily evaluated than similarities, as they are indicative of evolutionary specializations, and hence of divergence.

Conversely, the lack of a fossil record and thorough functional analyses renders similarities among different skulls or similar skulls in different birds more difficult

to evaluate, as there is no sure way to determine the degree of convergence present in the modifications exhibited.

Perhaps one of the most significant results of this study is the demonstration of the differential rates of evolution of the skull at generic levels among the major tyrannoid groups. As a corollary, it might also be noted that the degree of distinctness among most existing genera of tyrannoid birds themselves corresponds directly with the relative distinctness of the skulls and inversely with the numbers of genera in the various families and subfamilies.

Among the Tyrannidae, large numbers of similar genera have skulls exhibiting differences of considerably lesser magnitude than those among the cotinga assemblage. The skulls of tyrannid genera are often barely distinct. Within the Cotingidae, as presently constituted, the skulls are generically distinct, and often identifiable even to species. Skulls of the Pipridae are intermediate in being generically identifiable, if only on the basis of proportions. Male plumages are distinct, but females are often remarkably alike. The distinctness of the skulls of the three monotypic families parallels the distinctness of the birds based on their other characters.

As previously noted (see Table I), modifications in the skulls (including bill size and shape), plumage,

development of rictal bristles, as well as voice (hence probably structure of the syrinx) and courtship behavior, seem to be generally correlated with the habits and food preferences within the groups of tyrannoid birds.

Although many tyrannoids are to some extent omnivorous, the principal trends are towards fruit-eating among the Cotingidae, and insect-eating among the Tyrannidae.

Most of the aerial insect-catchers are birds of medium to small size and nearly uniform dull color, with bills usually more or less broadly triangular, depressed, and surrounded by well developed rictal bristles. Bright colors, if present, are generally confined to hidden coronal patches or to the lower underparts. This color pattern may render these predatory species relatively inconspicuous to their insect prey (as well as to bird predators) as they perch quietly on exposed vantage points. The flycatching habit seems to require few divergent modifications of the basic skull type possessed by birds with these habits, the principal variations being those of relative proportions of the bill, as well as absolute size.

Those insectivores that seek their prey on the ground or amid foliage usually have more slender bills and weaker rictal bristles. Pronounced sexual dimorphism in plumage is frequent. A greater variety of restricted feeding niches is probably available to birds of this type, and their skulls vary accordingly.

Fruit- and berry-eating tyrannoids are commonest in tropical and humid forests, where there is a great abundance of fruit- and berry-bearing plants of many types. This great variety of plant species provides a large number of feeding niches for frugivorous species. The birds presumably adapted to these relatively restricted niches vary greatly in size as well as structure of the skull. Bills are variable in size and shape, and rictal bristles are often reduced or absent. Extremes in sexual dimorphism are present, with brightly colored males predominating.

Many of the species of dense forest and brush are solitary birds and have loud, piercing calls. Since tropical areas are characterized by having many species of relatively low population densities (as contrasted with more temperate areas), these calls may be an adaptation for aid in communication in habitats in which the likelihood of females finding males of their species is otherwise relatively low. The conspicuous plumages, mouth linings, and ornamentation of the males of many of these species may serve as simple recognition patterns, as well as function as releasers of sexual behavior in courtship.

Students of the courtship and breeding behavior of the frugivorous tyrannoids (e.g., B. K. Snow, 1961, Procnias alba, Lipaugus cinereaceus, Perissocephalus tricolor; D. W. Snow, 1962b, Manacus manacus; Gilliard, 1962, Rupicola rupicola) have expressed the opinion that the fruit-eating

habit, requiring only a short daily period of foraging activity, has allowed these birds to develop the elaborate courtship patterns that occupy the males during the majority of the daylight hours. The same principle of temporal foraging economy has been suggested as responsible for allowing the female more time at the nest, thereby releasing the male from parental responsibility.

Observations of collectors in the field indicate that some species of the above groups (the fruitcrows, pihas, and manakins), all of which possess rictal bristles, feed on insects to a greater or lesser extent when not breeding. This duality in food selection may be a reflection of seasonal abundance of food sources instead of (or as well as) an expression of the temporal exigencies imposed by the method of courtship, rather than the reverse, as suggested above. Whatever the case, food habits, and hence cranial structure, are expressive of much of the total biology of the birds, and as such, cranial features appear to be of taxonomic value as a character complex within the Tyrannoidea. The level at which the skull is significant in this respect varies from group to group and is not the same across the broad spectrum of the superfamily.

With respect to the last, the point should be made that skulls may be subject to modification within the general groups to which they belong not only in relation to

differences in primary and secondary food preferences but also such nonfood-related functions as "gaping displays" and "bill-snapping" in courtship and the gathering of specialized nesting materials.

The Tyrannidae and Unsolved Problems

In comparison with the primarily frugivorous tyrannoids, the skulls of birds of the generally insectivorous groups are much less well differentiated. These skulls exhibit few highly developed modifications, and although undoubtedly specialized for a primarily insectivorous diet, may be considered more generalized skulls. Principal variations seem to involve size, bill shape and proportion, form and presence or absence of the nasal septum and its transverse "trabecular plate," ossification of the interorbital septum, and configuration of the palatines and cranium. Most of these variations are comparatively minor, relative to those in other tyrannoids, and may be encompassed among related species by individual variation.

A conception of the extent of individual variation is essential to the interpretation of similar skulls at lower taxonomic levels. In order for detailed studies of variation to provide a truly accurate picture, each species studied must be represented by a series of "matched specimens" alike in sex, age, and geographical locality compared with similar series from other areas. No such series was

available for study, other than the two series of Tyrannus mentioned in the discussion of the palatine process. Skulls of these series were rather uniform, but did not correspond well with other skulls of the same species in other collections. As no comparable series were available, no conclusions can be drawn concerning individual variation at the species level, and treatment of the insectivores must perforce be limited to genera and groups of genera.

In other tyrannoid groups greater morphological gaps exist at lower taxonomic levels and the lack of detailed knowledge of variation provides less of a barrier to taxonomic interpretation.

The generally larger flycatchers of the first three subfamilies of Hellmayr's arrangement lend themselves better to characterization than the remaining four, which, for the most part, contain the smallest members. The genera of the last groups are the most poorly represented in collections. In addition, the skulls are small and fragile, and a great many of those available for study were incomplete or damaged to a point that their usefulness was severely impaired.

Among the first three subfamilies, Tyranninae, Fluvicolinae, and Myiarchinae, a distinct dichotomy is evident.

The "tyranno-myiarchine" flycatchers, composed of the Tyranninae and Myiarchinae, s.s. (Myiarchus through

Xiphocolaptes) and Rhytipterna (from Cotingidae), form a relatively homogeneous group.

A second such group is composed of the Fluvicolinae, plus the remainder of the Myiarchinae, s.l. On the whole, these two last sub-groups probably are distinct from each other on the basis of characters too minor to justify their separation at a subfamily level, merging insensibly by way of a few intermediate genera (e.g., Ochthoeca, Ochthornis, and Entotriccus) and might represent terrestrial or semi-terrestrial and arboreal sections of the same stock. They may be worthy of only tribal rank within a single subfamily.

The first section of the Fluvicolinae (Agriornis through Neoxolmis) represents the terrestrial extreme, and the section of Myiarchinae from Nuttallornis through Myiophobus, the arboreal (or aerial) extreme. Savornis and Pyrocephalus, long of uncertain position, seem to belong with the second section.

The attilas are essentially tyranno-myiarchine, lacking the ossified interorbital septum. The becards seem also tyranno-myiarchine, lacking the interorbital septum as do the attilas, but having the premaxillae swollen between the nares.

The "basic" tyrannoid skulls (excluding for the moment Hellmayr's last four subfamilies and the becards) seem divisable into three possibly "subfamily-equivalent" groups: Attilinae, Tyranninae (including Myiarchinae,

s.s.), and Fluvicolinae (including the remainder of the Myiarchinae).

Perhaps largely as a result of insufficient material, the adequate characterization of the smaller flycatchers is, at the present time, impossible. A number of these forms may be referable to one or the other of the two major flycatcher groups treated above, leaving a "core group" of smaller forms, with "globular" crania, in which the bony interorbital septal element obliterates the supraorbital fenestra against the roof of the cranium and thus enlarges the infraorbital fenestra (Type 4 septum, see Table II).

The type of interorbital septum associated with many of the smaller flycatchers may not be basically correlated with smaller size, as indicated by the fact that the same type of fenestration is found among many of the larger furnarioid suboscines. In addition, Types 2 and 3 interorbital septa are found in some of the smaller flycatchers (which may or may not be misplaced in their present subfamilies). The Type 3 septum is characteristic of the manakins, which are of similar size.

Any division of the "core group," possibly according to the presence or absence of the plate in the nasal septum, must await the accumulation of more material, since many of the smaller skulls examined show indications of damage.

I rather doubt, however, that the separation of the

Euscarthminae from the Platyrinchinae, and the Serpophaginae from the Elaeniinae is justifiable at the level of the subfamily. An arrangement of two subfamilies, each with two sub-groups of tribal rank, might be more realistic. Onychorhynchus might be placed tentatively in the Platyrinchinae as a third tribe.

Relationships of the Tityras and Becards

As originally constituted, the subfamily Tityrinae contained the becards and tityras--"cotingas" with swollen bills and abbreviated ninth (penultimate) primary flight feathers in the males. Ridgway subsequently modified the tarsal descriptions from pycnaspidean to "semi-pycnaspidean" in Tityra (s.s.) and "quasi-taxaspidean" in "Erator" (Tityra inquisitor), Pachyramphus, and Platypsaris.

Modifications of the primary flight feathers, usually sexually correlated, are common among the Tyrannoidea, especially in the Pipridae and Rupicolidae (where they are sound-producing) and in the Tyrannidae. Attenuations of the tips of the outer primaries occur commonly in the Fluvicolinae and Tyranninae, often varying specifically within a single genus in number and degree. For example, in the genus Knipolegus all 10 primaries are attenuate in both sexes of aterrimus, the 10th alone in males of cyanirostris, and none in females of cyanirostris or either sex of anthracinus. Abbreviation of primaries occurs

sporadically, varying as in the following examples: primary 10 (outermost) in Alectrurus, Arundinicola, and Machetornis; 9, 8 in Lessonia; 8-4 in Chirocylla; 7, 6 in Pseudocolopteryx sclateri and P. dinellianus; 6, 5 in P. acutipennis.

Except for the unparalleled uniformity of reduction occurring among the Tityrinae, a feature as generally variable as that of the primary flight feathers would not likely prove a substantial unifying character at the level of any family-group taxon. Patterns of tarsal scutellation have been demonstrated to be variable (see discussion of Pipridae), variations of both the pycnaspidean and taxaspidean occurring in each of the two groups included. Ridgway's "semi-pycnaspidean" and "quasi-taxaspidean" are merely successive intermediate stages of increasing coalescence of the plantar scutellae intermediate between the typical pycnaspidean and taxaspidean types.

The tityras are stocky, short-tailed, robin-sized birds with swollen bills (see discussion under Nasal Region). Plumages are essentially black and gray in both sexes, although there is some brown in females and young males. T. semifasciata and T. inquisitor are known to nest in cavities "stolen" from woodpeckers (Skutch, 1946).

The becards are smaller, more flycatcherlike birds, with broad, swollen, and depressed bills. They, as well as the tityras, appear somewhat "large-headed." Most

species are distinctly dimorphic, the male plumages differing widely among species of both genera. Female plumages are more subdued, those of some species being "typically flycatcherlike," with wing-bars and patterns of brown, green, and yellow. Unlike the tityras, the becards build their own covered nests (Skutch, 1954).

Both groups form pair-bonds, in contrast to the more frugivorous cotingids and manakins.

The peculiar structure of the tityrine bill and nasal capsule, described in an earlier section, provides a character which, by its very uniqueness, constitutes a radical departure from an essentially conservative pattern that obtains throughout the tyrannoid series. In addition, nowhere else in the Tyrannoidea does the bill itself exhibit the dimensional departure from the tyrannoid norm as in Tityra cayana and T. semifasciata. The more depressed bill in T. inquisitor is closer in shape to those of the becards, as is the skull, which also carries a considerable degree of over-all resemblance to those of the becards.

Only in the tityras (and cocks-of-the-rock, whose position is otherwise controversial) has it been demonstrated that cranial characters have evolved at such a rate, relative to external characters, that skulls of species within a genus should be so easily distinguishable, either by a single character or by combinations of

characters.

Lack of knowledge of the functional implications notwithstanding, such a differential rate of evolution of the cranial character complex as that exhibited by the tityras, both within the genus and for the group as a whole, seems to imply the existence of a decided evolutionary separation between the tityras and the other Cotingidae.

A divergence such as that exhibited by the tityrine nasal capsule would appear to be to some extent indicative of status at least of family rank in the Tyrannoidea, particularly if supported by other characters.

Skulls of the becards are basically tyranno-myiarchine but also resemble very closely that of T. inquisitor, and to a lesser extent Querula. The palatines are tityrine and the ossified nasal capsule of Platypsaris exhibits a short partially tubular lateral extension of the naris, probably correlated with the swelling of the bill. Examination of the unossified capsular region in Pachyramphus skulls showed indications of a less developed but similar structure. Other suboscine genera with superficially similar swollen bills (e.g., Rhynchocyclus, Sapayoa, and Smithornis) show no indications of similar modifications of the nasal region, either in the manner of premaxillary expansion or modifications of the wall of the capsule itself.

The over-all similarity of the skulls of such birds as

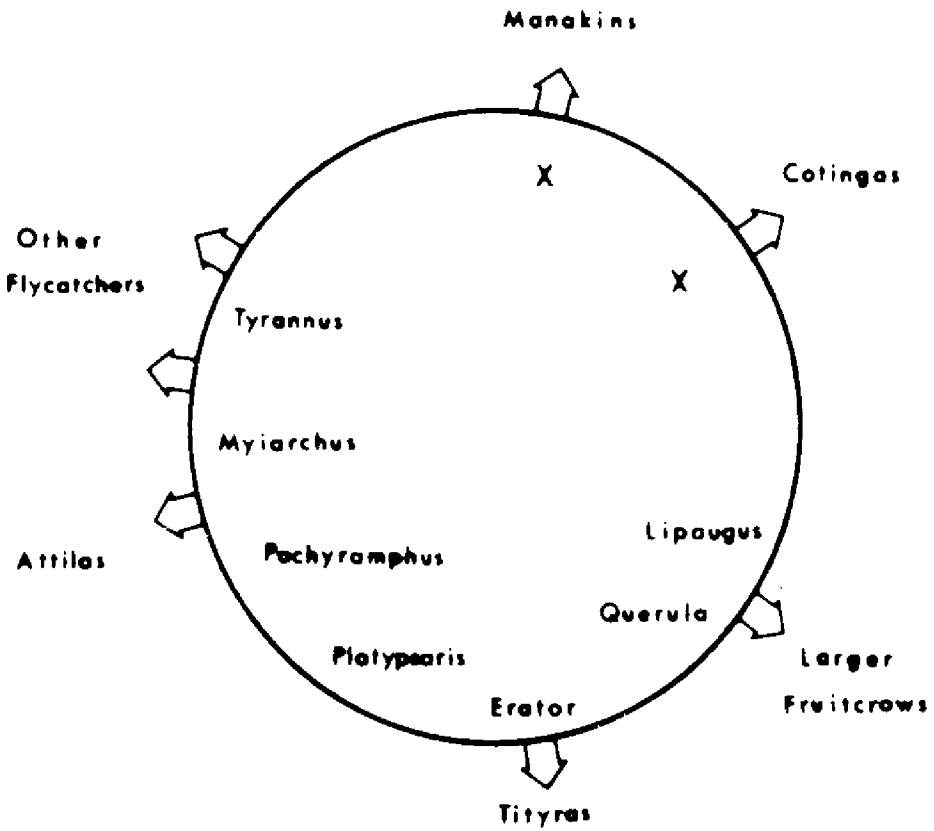
Querula and Lipaugus, at least subfamilially distinct from those of T. inquisitor, the becards, and the flycatchers, seems to indicate that these skulls might constitute a rather basic type. The combination in the tityra and becard skulls of the unique nasal capsule, internasal premaxillary swelling, and free palatomaxillaries tending towards fusion with the prepalatine bars, seems to indicate a lack of especially close relationship between these birds and the others mentioned above.

Should Querula eventually prove closely related to the tityras and becards, the common form of skull may be a basic type for a number of others. Figure 11 shows a possible relationship for some of the Tyrannoidea. This "assemblage" would be consistent with much of the cranial evidence, as well as whatever evidence can be provided by the standard character of tarsal scutellation (see Figure 12). Several of the genera whose position has been controversial because of ambiguous scutellation are included here.

The Status of the Pipridae

According to Ridgway's diagnoses (1907: 328-329; 335-340; 723-724; 769-771), the Pipridae agree with the Cotingidae in the nature of the insertion of the syringeal musculature (catacromyodian; anacromyodian in Tyrannidae), and greater development of the femoral artery, as opposed

Figure 11. Possible Derivation of Some Tyrannoidea Based on Type I and III Skulls. Genera within the circle are not presumed to be ancestral to others, but may be closer in structure to a possible ancestral type or group represented by the circle.


Manakins
Cotingas
Other
Flycatchers
Tyrannus
Myiarchus
Attilas
Pachyramphus
Lipaugus
Querula
Larger
Fruitcrows
Platypsaris
Erator
Tityras
X
X

to the sciatic (heteromerous; homeomerous in Tyrannidae). They agree with the Tyrannidae in the possession of an exaspidean tarsal envelope (variable in Cotingidae but never exaspidean; see below). The Pipridae differ from both Tyrannidae and Cotingidae in a slightly greater syndactyly of the middle and outer toe (or middle and inner in one genus, Piprites).

At the time of Ridgway's work the then supposedly diagnostic "internal characteristics" were too poorly known for them to be of help in his allocation of the great majority of the genera with which he had to deal. The degree of pedal syndactyly was deemed by him (op. cit., 270) too variable to be of any general application, leaving the pattern of tarsal scutellation as "the only available external character."

According to information in Sclater (1888) the character of the tarsal envelope apparently was responsible for the removal of Cabanis' (1859) subfamily Piprinae from the Cotingidae and its elevation to family rank by Sclater and Salvin (1873) in their Nomenclator.

As Ridgway himself pointed out (op. cit., 770), the Cotingidae are not pycnaspidean alone, as Sclater apparently believed, but possess no less than three types of tarsal envelopes, holaspidean, "modified taxaspidean," and pycnaspidean. The exaspidean type of the Tyrannidae was also recognized as variable, often approaching the

pycnaspidean ("ultra-exaspidean to semi-pycnaspidean").

Ridgway does not appear to have been satisfied with the adequacy of tarsal scutellation as the principal diagnostic character (op. cit., 337-338) but apparently felt compelled to rely upon it quite heavily in the absence of anything else. His rigid reliance upon this single character resulted in the removal of four species from their genera in the Tyrannidae (Myiarchus validus, Elaenia elegans, Pogonotriccus zeledoni, and Tyrannulus semiflavus) and the erection of new genera for their reception (Hylonax, Elaeniopsis, Idiotriccus, and Microtriccus). The reallocation of these and, for similar reasons, other genera among the families of the Tyrannoidea and other families further removed was recommended. These changes by Ridgway are summarized below:

Lawrencia (acutiplantar), Tyrannidae to Vireonidae;

Stigmatura, Hapalocercus (taxaspidean), Muscigralla (holaspidean), Tyrannidae to Formicariidae;

Culicivora ("non-exaspidean"), Tyrannidae possibly to Furnariidae;

Habrura (taxaspidean), Sirystes, Hylonax (holaspidean), Idiotriccus ("ultra-pycnaspidean"), Elaeniopsis, Tyrannulus, Microtriccus ("essentially pycnaspidean"), Rhamphotrigon, Ornithion, and Xenopsaris ("not exaspidean"), Tyrannidae to Cotingidae;

Laniisoma, Pipridae to Cotingidae;

Rupicola, Rupicolidae to Cotingidae;

Laniocera (exaspidean), Cotingidae to Pipridae.

Hellmayr (1927: iii) was unable to accept the use of a character so variable even at the species level as the tarsal envelope as a basis for removing the above genera from the proximity of others they so closely resembled and their placement in groups in which they otherwise did not seem to fit. Accordingly, he chose not to accept most of Ridgway's recommendations and returned all but Lawrencia and Laniisoma to their former positions. He did, however, retain Hylonax and Microtriccus as distinct genera within the Tyrannidae.

Rand (1959), in a broad survey of tarsal scutellation among the families of oscine passerines, found sufficient variation in this character to render it unusable, in most cases, as a key character at the family level. Ridgway was similarly unable to use this character below the family level, although he apparently attempted to create greater uniformity at that level by arbitrarily reallocating the most "troublesome" genera.

Rand (op. cit., 275) presumed the pycnaspidean pattern to be a primitive condition from which the various oscine tarsal types developed through the enlargement and coalescence of the smaller, independent scutellae of the pycnaspidean type.

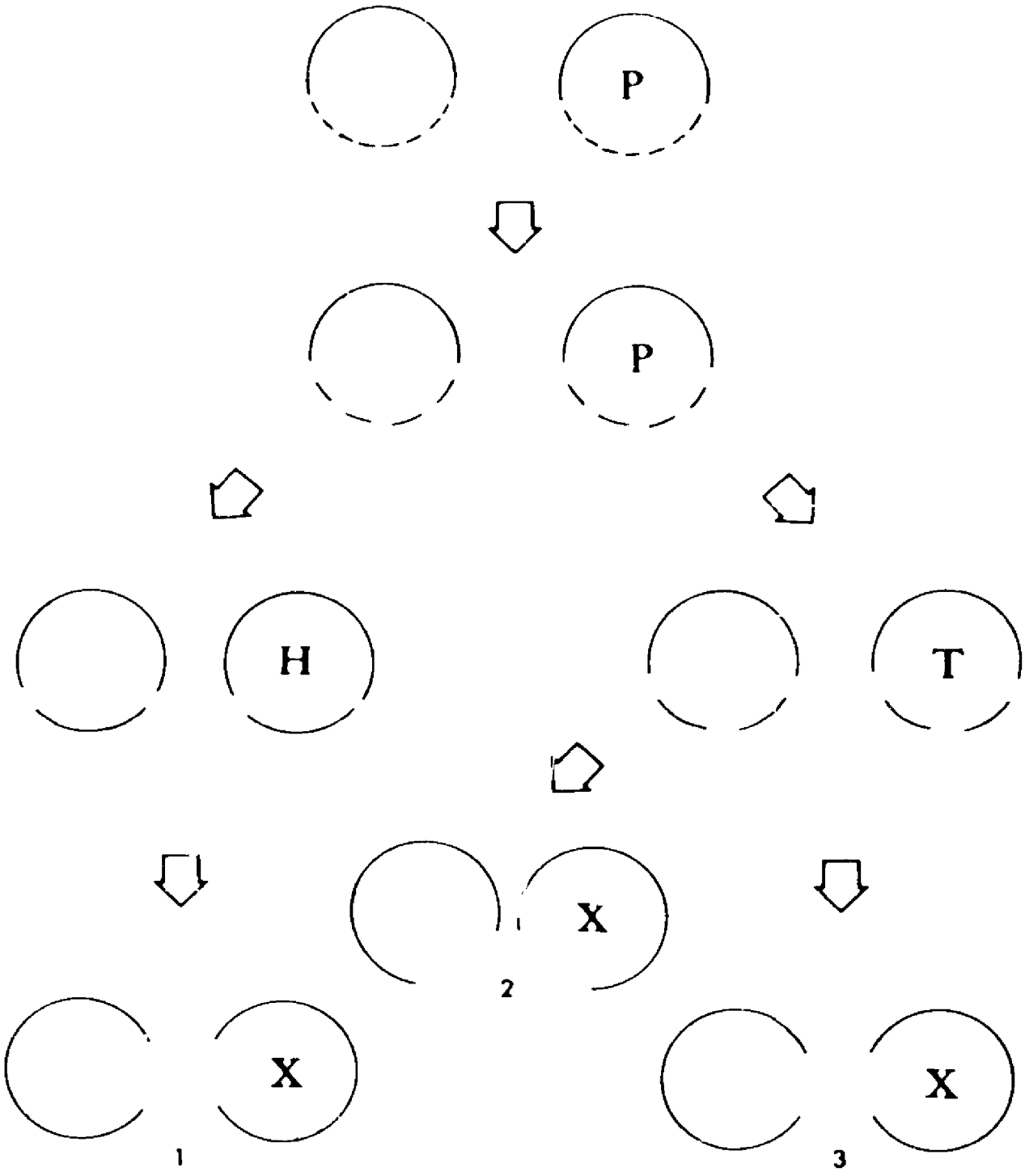
The same form of modification could well have occurred within the tyrannoid assemblage, the exaspidean type arising independently more than once (Figure 12). Obviously, the possession of the exaspidean tarsal type by both manakins and flycatchers has not been deemed evidence of sufficient importance to unite these two families, even by Sclater, since a close relationship between manakins and cotingas does not appear to have been seriously questioned. Indeed, most monographers of the groups have maintained the separation of the Pipridae only with reservations.

Since the Cotingidae were demonstrated by Ridgway to possess three tarsal types, it does not seem inconsistent that a fourth be included. Neither does it seem entirely consistent that Hellmayr, who did not recognize the generic reallocations made by Ridgway largely on the basis of tarsal scutellation, should have maintained the Pipridae, apparently elevated by Sclater on the same basis.

The only other character relied upon by Ridgway, the greater degree of syndactyly of the toes, likewise has been demonstrated by Ridgway himself to be similarly variable, and seems to have been treated accordingly by Hellmayr.

Except for the terminal section of the Pipridae (in Hellmayr's arrangement), the morphology of the manakin skulls seems to represent less of a departure from that of the typical cotingas than does that of other major groups generally included within the family, and insofar as is

Figure 12. Hypothetical Derivation of Exaspidean Tarsal Scutellation Among the Tyrannoidea (not a phylogeny). Symbols: P, pycnaspidean; T, taxaspidean; H, holaspidean; X, exaspidean; 1, most Tyrannidae; 2, Euchlornis; 3, Pipridae. Diagrams represent cross-sections of tarsi. Pycnaspidean tarsi occur in Rupicolidae, Phytotomidae, Cotingidae (Querulinae, Gymnoderinae, and some Cotinginae, Tityrinae, Lipauginae, and Attilinae), and some Tyrannidae (a few Myiarchus); taxaspidean in Cotingidae (some Cotinginae, Tityrinae, and Attilinae); holaspidean in a few Cotingidae (some Lipauginae and Attilinae) and Tyrannidae (Sirystes and some Myiarchus); and exaspidean in Pipridae, some Cotingidae (Euchlornis and a few Attila), Tyrannidae, and Oxyruncidae. More than one type may occur in large series of one species (e.g., Attila spadiceus, pycnaspidean, holaspidean, exaspidean), or on a single tarsus of one individual (e.g., Platyrinchus coronatus, taxaspidean and pycnaspidean; Myiarchus crinitus, holaspidean and exaspidean).


P
P
H
T
X
X
X
1
2
3

presently known, seems consistent with the other external characters generally used. Garrod's (1877b: 526) conclusion, reached after examination of a number of suboscine syringes, is particularly applicable here: ". . . that the Pipridae and Cotingidae should be considered to be different families is not borne out by the nature of the lower larynx; and it seems hardly possible to allow a difference in tarsal scutellation to constitute a family difference, when not borne out by more important points of internal structure."

On a strictly anatomical basis (upon which the family was originally defined), there seems at present little really substantial foundation for the retention of the Pipridae as a family distinct from the Cotingidae as this extremely diverse family is now constituted. A really consistent approach would seem to require either a reduction in rank for the Pipridae and a return to their previous status as a subfamily within the Cotingidae, or else a fragmentation of that heterogeneous family into a number of smaller, more homogeneous family units.

With the exception of Tyranneutes, the Piprinae of Sclater's (1888) arrangement examined in this survey form a close-knit group of small birds with usually brightly colored males and dull-colored females. Males of some species have variously modified wing and/or tail feathers. Many species share an unusual method of courtship ("arena

behavior"). The genera of this group of manakins have relatively uniform skulls separable from the Cotinginae examined only on relatively minor characters.

The terminal section of the Pipridae in Hellmayr's arrangement (Massornis through Heterocercus, less Sapayoa, undescribed until 1903), plus Laniisoma (= Ptilochloris, Family Cotingidae), is the equivalent of Sclater's (1888) subfamily Ptilochlorinae. The Ptilochlorinae, or "aberrant manakins," were a heterogeneous assemblage of tyrannoid genera comprising ". . . a small set of mostly dull-colored birds, which combine the foot-structure of the Pipridae with the bill of the Tyrannidae" (Sclater, 1888: 316).

The above genera, plus Tyranneutes, need further investigation; a number possibly do not belong among the manakins.

Skulls of Tyranneutes, Neopelma, Sapayoa, and Schiffornis have been examined. Tyranneutes and Neopelma skulls bear resemblance to those of flycatchers. Schiffornis skulls do not resemble closely those of the manakins, but are otherwise difficult to place; they are more similar to those of the Cotinginae than to those of the Pipridae.

Information gathered by Sick (1959) and Snow (1962a) indicates that there are behavioral similarities between some of the manakins and a few smaller flycatchers and

cotingas. The nature of the skulls of Neopelma and Tyranneutes, intermediate between those of some smaller flycatchers and the more "typical" manakins, coupled with less elaborate courtship performances and more flycatcher-like general appearances, might be taken to suggest some sort of flycatcher-manakin relationship. This possible relationship, plus the already known morphological cotinga-manakin relationship for the dimorphic manakins, might further indicate an intermediate position for the Pipridae between the other two families.

The Enigma Manakin, Sapayoa aenigma, externally appears flycatcherlike, but its skull is unique among all the Tyrannoidea examined. In several characters it bears resemblances among other suboscines only to Smithornis, one of the only two African genera of Eurylaimidae. The remaining genera of eurylaimids are essentially Indo-Malaysian.

Interesting is the fact that the Smithornis skull is intermediate in structure between Sapayoa and some of the Asiatic eurylaimids, and the Smithornis has a sternum with a bifurcate manubrium (spina externa). The Eurylaimidae were once considered related to the Cotingidae (see Pycraft, 1905) but have been maintained as a separate suborder largely on the presence of a nonbifurcate sternal manubrium and the presence of a plantar vinculum (a small connection between the flexor tendons of the toes). As

pointed out by Pycraft (op. cit.), the vinculum is not possessed by all eurylaimids, nor is the bifurcate sternal manubrium universal among the Cotingidae; the major artery of the thigh is the femoral, as in the Cotingidae and Pipridae, and the syrinx (as then known) agrees in its major features with the latter families.

Of the Eurylaimidae, Corydon, Cymbirhynchus, Eurylaimus, and Calyptomena have been described by Pycraft (1905). I have examined one skull each of Corydon sumatranus, Calyptomena viridis, and Smithornis capensis, as well as two of Sapayoa aenigma. The skulls of Corydon and Calyptomena agree with Pycraft's descriptions.

The principal points of cranial similarity between Sapayoa and Smithornis, in addition to the general conformation, involve correlation of modifications of the antorbital complex and maxillopalatines.

In the above eurylaimid genera, the maxillary process of the nasal is swollen dorsally, and braced against the laterally expanded frontal plates. The lacrymal, present in Calyptomena and Smithornis, appears to be absent in Corydon, Eurylaimus, and Cymbirhynchus. In Smithornis and Sapayoa, the frontal plates are not enough expanded laterally to reach the swollen "frontal process" of the nasal. In the last two genera, the head of the lacrymal is expanded dorsally and medially, replacing the frontals above the lateral portion of the nasals (Figure 13). In

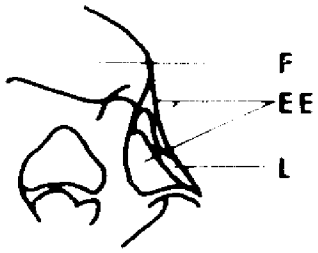
Figure 13. Cranial Features of Sapayoa and Representative Eurylaimid Genera. Figure 13a, b, Sapayoa; c, d, Smithornis; e, f, Calyptomena; g, h, Corydon. Symbols: EE, ectethmoid; F, frontal; L, lacrymal; N, nasal.

a

b

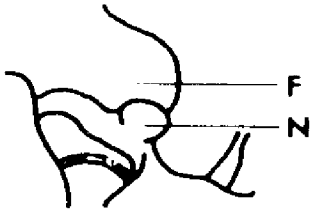
c

d



e

f



g

h

Calyptomena and Smithornis, the ectethmoid plates are laterally expanded and swollen, with the lacrymal displaced to the anterior surface of the ectethmoids. The ectethmoids of Sapayoa are even more expanded laterally, and the ventral portion of each lacrymal is absent (or greatly shortened), extending only part way down the edge of the ectethmoid.

The maxillopalatines in Sapayoa and the eurylaimids are reduced from the typically broad suboscine condition to slender stalks, capitate at the tip. In addition, these processes are peculiarly arched above the prepalatines, descending medially beneath the end of the vomer.

Reduction of the maxillopalatines, as in the above pedunculate condition, occurs only rarely among suboscines, although it is the common condition in the oscines. Except in Sapayoa, pedunculate maxillopalatines have not been found among the Tyrannoidea examined in this study.

The lacrymal in the Tyrannoidea is a remarkably consistent character, varying only in relatively minor proportional details (cf. key to the skulls of Tyranni in the introductory section). Nowhere else among the tyrannoid skulls examined does the lacrymal occur in the form present in Sapayoa, and only among the eurylaimids, of all suboscines examined, does the antorbital complex occur modified as described above.

No family of suboscine passerines is recognized to

occur in both Eastern and Western Hemispheres. Since inclusion of Sapayoa in the Eurylaimidae would extend the known distribution of that family to the New World, Sapayoa should probably remain incertae sedis among the Tyrannoidea until its affinities can be investigated more thoroughly.

The Larger Fruit-eaters

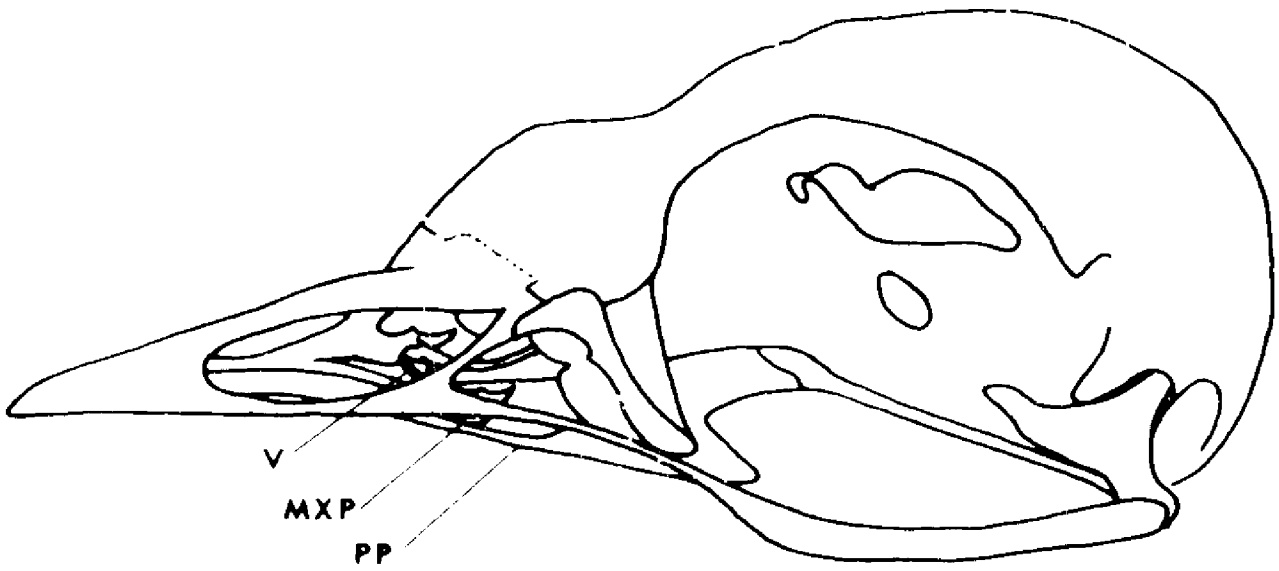
Skulls of the larger fruit-eaters fall into three major groups, represented in the highest degree of specialization by Rupicola, Cephalopterus, and Procnias. Skulls of birds comprising at least the latter two groups possess several modifications apparently designed to resist upward pressure against the palatal surface or to facilitate a large gape, or both.

Procnias and Cephalopterus

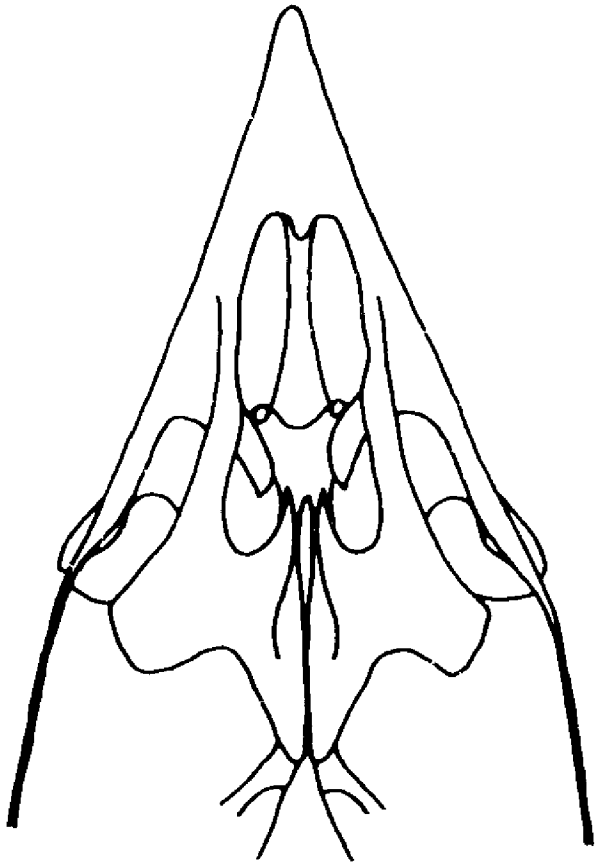
In Procnias (Figure 14), the vomer is expanded at the free end, slightly decurved, U-shaped in cross-section, and recumbent on the upper surface of the inflated maxillopalatines. The maxillopalatines, stronger than in any other cotinga, are thicker behind than in front, being between crescentic and L-shaped in cross-section, and rest firmly on the upper surface of the prepalatine bars.

Anterior to the maxillopalatines the prepalatines are weak, but they expand rapidly to the posterior, joining an expanded and flattened palatine plate formed by greatly expanded trans-, inter-, and post-palatine processes.

Figure 14. Skull of *Procnias nudicollis*.
Figure 14a, lateral aspect; b, palatal aspect.
Symbols: MXP, maxillopalatine; PP, prepalatine bar;
V, vomer.



a



b

Above the palatine plate each mediopalatine rests along its entire length against the lower surface of an inflated ectethmoid plate.

The parasphenoidal rostrum, which supports the palatine complex, is joined above by a heavily ossified interorbital septum. Thus, the broad palatine plate seems to be braced against compressive forces from below by the vomer and maxillopalatines anteriorly, and the ectethmoid plates and interorbital septum posteriorly. The ectethmoid plates, in addition, may be reinforced from above by the large, arched, frontal plates.

As demonstrated by Fisher (1955) and Bock (1964), kinesis cannot always be accurately measured or interpreted without knowledge of the muscles and ligaments that bind together the movable and immovable elements of the skull, thereby limiting the movement of these parts. A few features that probably influence kinetic operation are present, as determined by manual operation of skulls softened by immersion in warm water.

The head of the lacrymal fits into an obvious notch at the top of the maxillary process of the nasal bone, apparently forming a retractor stop, such as that demonstrated by Fisher (1955) in Corvus. Beneath the frontonasal hinge, two opposing medial bony inflations are present, and may serve a similar function.

The inferior turbinals are elongate but rarely are

even weakly ossified, and they extend to the ectethmoid wall, with which they seem to articulate via a bony tubercle on each ectethmoid. While such a condition as the last, in an unossified nasal capsule, may be unrelated to kinesis, the presence even of unossified turbinals abutting the ectethmoids would seem to indicate the presence of retractor stops elsewhere to protect these structures from injury, and supports the inference of this function for the lacrymal.

Bellbirds are known to possess a large gape, utilized by the males to display their pigmented mouth-linings in courtship (B. Snow, 1961; Slud, 1964). The large gape may also facilitate the consumption of large fruits.

Although the skull and mandible of Procnias seem too weak to exert much force for crushing or plucking large fruits, the modifications of the palate and their associated inferentially supportive features may be designed for protection of the eyes, nasal capsule, and generally light bony structure of the skull itself. The temporal fossae are relatively shallow, indicating weak mandibular adductor muscles.

The compressed form of the parallel, ventrally bowed quadratojugal bars probably resists bending behind the level of the lacrymals and may allow a horizontal push on protraction of the quadrates. Each bar becomes compressed and weakened below and in front of the lacrymal, forming an

interosseus hinge, with the expanded foot of the lacrymal acting as fulcrum on protraction of the bill. The prepalatines, weakest ahead of the maxillopalatines, appear to bend over the maxillopalatines. This combination of interosseus hinges appears to allow greater protraction than straight and unbending bones.

The skull of Procnias could have been derived by a simple progression of modifications from a type similar to the cotingine skull, which possesses similar but less developed modifications, more naturally than from any other cotingid type. Cephalopterus represents a type similarly derivable from one resembling either Querula or Lipaugus.

Cephalopterus has a skull that is larger, stronger, and of entirely different conformation than that of Procnias. The palate (Figure 4d) is equally different but possesses inferentially similar supportive modifications that parallel in possible function those of Procnias, with the following differences: the maxillopalatines are massive, but thin in cross-section, and do not contact the prepalatines; the prepalatines are slender, but rodlike, and are incapable of bending except possibly at the expanded, platelike anterior end. In addition, the lower ectethmoid bullae drop below the level of the quadratojugal arches medially (although resting on them laterally), forcing the palatines to twist downward laterally. The palate is thus arched in cross-section, and the

prepalatines rise at an angle to meet the premaxillae. The quadratojugal arch is straight and is broadly flattened at the maxilla.

Similar retractor stops appear to be present, but protraction seems less extreme and is accomplished through different modifications. Although largely fruit-eaters, all fruitcrows, regardless of size, possess strong rictal bristles and are known to take insects as a part of their diet. Bellbirds lack rictal bristles and are not known to eat insects. Skulls of the fruitcrows are stronger, with longer bills, and seem better able to exert compressive forces. These skulls have deep temporal fossae, implying strong adductor muscles.

The degree of specialization exhibited by each of these extreme types, apparently traceable by progressive modifications along different lines, indicates a broader gap in relationship between the bellbirds and fruitcrows than would be implied by their past inclusion within the same subfamily.

Rupicola

Skulls of the two species of Rupicola differ on an intrageneric level to a degree unparalleled among the Tyrannoidea so far examined (Figure 7g). R. rupicola is unique among the Tyrannoidea in the arched, compressed bill and its associated modifications. The nasal capsule of Rupicola has been described in an earlier section. The

oblique, unfolded alinasal turbinals fuse directly to the maxillopalatines (which are twisted nearly to the vertical at the tips) rather than joining, as in other tyrannoids, the vomerine horns. Figure 10a shows the vomerine "horns" of the juvenile R. peruviana skull to be separate centers of ossification. These separate ossicles evidently become incorporated into a maxillopalatine-alinasal complex, fusing with the latter two elements into a single bony continuum in the adult skull. The vomer is free of these "compound maxillopalatines," and has an oblique facet on each corner. These oblique facets nestle into a pair of bony braces formed by the maxillopalatines below and the alinasal turbinals in front. Behind this point, the vomer is narrow and tubular in section (possibly as a result of the inturning of the sides of an "originally" U-shaped vomer). There is thus a strong, tripartite joint formed by the two compound maxillopalatines and the tubular vomer. The turbinal elements of the compound maxillopalatines are further braced by heavily ossified capsular walls to which they are firmly united. A fourth element may also contribute still another brace. The heavily ossified nasal septum, internally braced by its trabecular plate, contacts the vomer from above.

The prepalatines are narrow anteriorly and expand gradually to the rear. The ectethmoids are not inflated, but the palatines are arched and depressed posteriorly by

downward protrusion of the ectethmoids (Figure 7g), as in Cephalopterus. Strong, truncate transpalatines (absent in R. peruviana) recurve around the ectethmoid protrusions, giving the palatine a W-shape when viewed from front or rear. The prepalatines are braced anteriorly by the twisted maxillopalatines. The interorbital septum is ossified, the transpalatines are slightly flattened, and the interpalatine scrolls are widely spread.

A further unique feature, described in a previous section, is a free palatomaxillary arising posteriorly from the maxillary mass behind the maxillopalatine.

Retractor stops, similar to those described above, are apparently present, although the head of the lacrymal in R. rupicola is hook-shaped. The temporal fossa is moderate in depth. The quadratojugal arches are nearly straight. The cranium is depressed, and the frontals are folded forward over the base of the bill.

The possibility exists that some of the above modifications may have a role in one or more secondary functions of the bill in addition to, or instead of, the primary function of fruit-eating. During courtship, the male birds produce a loud snap by rapidly opening and closing the bill (Gilliard, 1962). Secondly, the female builds a large nest of rootlets and a few leaves plastered together with mud. One such adobelike nest was found by Gilliard to weigh 8 1/2 pounds.

Since palatomaxillaries occur in manakins (which also engage in "bill-snapping") and in aerial insect-catchers, these structures may be an adaptation for a rapidly closing bill.

The arched and compressed form of the bill, together with its internal system of bracing, may be associated with mud- and root-gathering.

The point should be made that each of the above activities is engaged in by only one sex. Of 12 R. rupicola examined, all were males; of 18 R. peruviana, only 2 were sexed as females. Skulls of these two did not seem to differ appreciably from those of the males.

R. peruviana differs from R. rupicola as follows: Cranium less flattened; bill anterior to naris relatively larger and less arched; frontals less folded over bill; nasal capsule covered with second layer of bone continuous with bill surface. Transpalatines absent (small adherent ossicles present, probably representing separate transpalatine centers of ossification (see Figure 10b). Cap of lacrymal complete, not hook-shaped; foot of lacrymal shorter. Interpalatine scrolls absent; postpalatines not flattened. Temporal fossae deeper.

A compound maxillopalatine similar to that of Rupicola is found in the Crimson Fruitcrow, Haematoderus militaris, which is otherwise dissimilar. This feature is taken to be convergent.

The highly specialized nature of the skulls of Rupicola and their relatively great interspecific differences are indicative of a decided evolutionary gap between the genus and the members of the Cotingidae, as also are the bizarre appearance and behavior of the birds, but cranial morphology offers no basis for placement of the genus in any other family.

The above discussions of skulls of frugivorous birds are all highly speculative, and the suggestions presented must remain tentative, pending thorough functional analyses and studies on the living birds. It is hoped that the ideas presented will encourage collectors in the field to pay greater attention to the foraging behavior and stomach contents of the birds they collect. Detailed information of this sort is lacking for all but a handful of tyrannoids, and even the most thorough functional analyses would be weakened without data of this type.

TAXONOMIC CONCLUSIONS

Introduction

The appearance after 1950 of several "conflicting classifications" led Bock to call for an end to speculation on the phylogeny and evolution of passerine birds "until enough evidence has been gathered to establish a classification acceptable to most workers" (Bock, 1960: 365). He stated that the best way to arrive at such a classification would be through the evaluation of studies of a series of several dozen single characters. Each of these single character studies he advises should be presented without taxonomic conclusions in order to avoid premature interpretations, despite the fact that many years might elapse before sufficient information would be available to permit the formulation of an acceptable classification.

Ideally, a perfect classification is expressive of natural relationships. Beyond that, it expresses the phylogeny of the organisms with which it deals. Without the ability to "travel back in time," enough information for the latter purpose can never be gained. This is especially true of a group like the passerine birds, for which the fossil record holds so little promise. Systems of classification evolve even as do the organisms their

authors seek to categorize. Each addition of a body of new information calls for a reevaluation of the preceding steps in the developing classification. Accordingly, I feel that taxonomic conclusions should be offered. Whether they are acceptable is another matter.

In an attempt to move one step nearer to a more natural classification of the group, I shall endeavor to integrate the information I have obtained from my investigations of tyrannoid skulls into the "purely provisional" schemes that have been proposed previously. My intention is that these modifications will serve to improve the framework within which information gathered in other studies can be integrated.

The use of subfamilies throughout the Tyrannoidea was standard among systematists preceding Ridgway. Ridgway did not further subdivide the Tyrannidae and Cotingidae, perhaps because he dealt only with the species occurring north of the South American continent. Hellmayr continued to use subfamilies for the Tyrannidae but not for the Cotingidae or Pipridae. Since the great diversity of skull types among the Cotingidae corresponds so closely to the old subfamilies, I have found the reinstitution of these convenient and, I believe, natural groupings to be advisable.

Family-group taxa have been used loosely in the ornithological literature. Many of the older treatments

are mere lists, without annotations. Either the originality of, or the precedent for, the taxa used is often impossible to ascertain. The authors and dates given for the family-group names used to introduce each of the following discussions, unless included in the "literature cited," are given on the authority of Gray (1869).

Family TYRANNIDAE Cabanis 1847
Subfamily TYRANNINAE Swainson 1837
Pitanginae von Ihering 1904
Tyrannina Swainson (vide Vigors, 1825)
Subfamily MYIARCHINAE von Ihering 1904
Onychorhynchinae Heine and Reichenow 1882-1890
Subfamily FLUVICOLINAE Swainson 1837
Taeniopterinae Gray 1841
Alectrurinae Gray 1847
Subfamily PLATYRYNCHINAE Burmeister 1856
Rhynchocyclinae Berlepsch 1905
Subfamily EUSCARTHMINAE von Ihering 1904
Triccinae Heine and Reichenow 1882-1890
Subfamily ELAENIINAE Cabanis 1859
Subfamily SERPOPHAGINAE von Ihering 1904

Skulls of birds of the Tyranninae and Fluvicolinae each form relatively distinct and uniform groups, while the Myiarchinae seem a heterogeneous assemblage, with Myiarchus and Eribates like the Tyranninae (particularly Sirystes and Legatus, as well as Rhytipterna), and Onychorhynchus like the Platyrynchinae and Todirostrum section of the Euscarthminae. The remainder of myiarchine skulls examined are more like those of the Fluvicolinae (particularly Entotriccus, Ochthornis, and Ochthoeca). Savornis and Pyrocephalus are like Contopus and Empidonax. The long-tailed nonterrestrial fluvicolines Gubernetes, Yetapa, and Colonia

(and probably Alectrurus, not examined), form a distinct subsection.

The Euscarthmlnae grade into the Platyrynchinae via Todirostrum and Oncostoma, and the Serpophaginae (via Serpophaga) into the Elaeniinae.

The uniformity of flycatcher skulls, contrasted with the heterogeneity of those of the cotingas, does not support the subdivision of the flycatchers at the subfamily level by cranial characters alone. Since the von Ihering-Hellmayr scheme, as outlined above, is based on both biological and external morphological features, a possible "compromise" might be in order. The following scheme is not formally proposed as a revised classification but is presented merely as a model for other workers:

Tyranninae
Fluvicolinae
  Fluvicolini
  Alectrurini
  "Contopini"
Platyrinchinae
  Onychorhynchini
  Platyrinchini
  Euscarthmini
Elaeniinae
  Elaeniini
  Serpophagini

Family PIPRIDAE Vigors 1825

The manakins, as do the cocks-of-the-rock, possess a highly developed communal courtship, with concommitant behavioral and morphological modifications referred to in earlier sections. This similarity in behavior had led

earlier workers to consider the two groups confamilial. Gilliard (1962), after a detailed study of the courtship behavior of Rupicola rupicola, believed the two groups convergent in behavior.

The courtship behavior of the three species of frugivorous cotingas studied by B. K. Snow (1961) is far less developed as a form of arena or lek behavior, though she thought it might be of this form in at least two of the species, Lipaugus cinereaceus and Perissocephalus militaris.

There is no apparent morphological evidence sufficiently strong to justify uniting the manakins with either the cocks-of-the-rock or the fruitcrow group of cotingas, in which Snow's species apparently fall. The behavior of members of the Cotinginae, which manakins resemble most in cranial morphology and plumage, is too poorly known to provide any evidence pro or con. Despite the similarity in internal morphological features, the Pipridae should be retained as distinct until the biology of the Cotinginae is better known.

Most authors who combine the two families place the manakins within the Cotingidae. According to Articles 23 and 36 of the International Code of Zoological Nomenclature (1964), Pipridae apparently has priority over Cotingidae as a family-group name by several years. As the reverse course would be contrary to general usage, should the family rank of the Pipridae prove untenable, a decision of

the International Commission would be necessary to validate the name Cotingidae for the combined families (Article 23d).

The genera Massornis, Schiffornis, Sapayoa, Neopelma, Heterocercus, and possibly Tyranneutes, are poorly known and require further investigation, but their placement in the Pipridae is questionable. On the bases of external appearance and cranial morphology, Neopelma could easily be placed in the Tyrannidae and probably should be transferred. Sapayoa bears no resemblance to the Pipridae other than the structure of the feet and legs. Externally it is flycatcherlike, but its skull is unique, resembling only that of Smithornis (Eurylaimidae). Sapayoa probably should remain incertae sedis among the Tyrannoidea until its affinities can be clarified.

Family COTINGIDAE
Ampelidae Swainson 1837
Cotingidae Bonaparte 1849

Subfamily COTINGINAE
Ampelinae Swainson 1837
Cotinginae Bonaparte 1849
Calypturinae Reichenow 1914

This subfamily contains the "typical" cotingas of the genera Euchlornis, Cotinga, Xipholena, Carpodectes, Heliochera, and Zaratornis, skulls of which have been examined in this survey and found to form a fairly natural group, plus Doliornis, Tijuca, Ampelion, Porphyrolaema, and Ampelioides, skulls of which have not been seen. Iodopleura and Calyptura (Calypturinae of Reichenow), long of

questionable affinities, are included in this sequence by Hellmayr, as are Phoenicircus and Laniisoma. Skeletons of these genera have not been seen. Phoenicircus previously had been associated with Rupicola. Laniisoma has the same peculiarly shaped bill as Attila, with a sinuate commissure, and surrounded at the base by bristles. Laniisoma may be allied with Attila and hence properly assignable to the Attilinae.

Subfamily GYMNODERINAE Gray 1847
Coraciinae Bonaparte 1850

As restricted by Salvin and Godman (1891), this subfamily contains only the monotypic genus Gymnoderus.

Gymnoderus foetidus is an aberrant species having short, velvety feathers on the head and a bare neck with only sparse feathers above and below. The male develops wattles on the bare throat. The Bare-necked Grackle is a largely black, crow-sized bird, nearly as large as the bigger fruitcrows and umbrellabirds with which it was previously united. It has a weaker bill and is nearly unique among passeriform birds in the possession of powder-down tracts.

The skull is a large form of the Cotinga type and the subfamily probably should be placed closer to the Cotinginae than to the Querulinae. The aberrant noncranial characters suggest that the genus should remain as a distinct subfamily rather than be united with the Cotinginae.

Subfamily PROCNIATINAE new subfamily

The genus *Procnias* contains four well-defined species of bellbirds, three of which have inflatable wattles or "caruncles" on the head or throat as part of the strong sexual dimorphism of the males. Bellbirds have a unique, loud, ringing call-note that gives them their common name.

Prior to the time of Salvin and Godman, the billbirds had been placed in the Gymnoderinae, along with the fruit-crows and umbrellabirds. Salvin and Godman (1891) removed *Procnias* (*Chasmorhynchus*) from the Gymnoderinae but transferred it to the Cotinginae, characterizing it as follows (*op. cit.*, 142): "The genus *Chasmorhynchus* has no near allies, so much so that its position in the family is by no means satisfactorily settled; there are even points in its structure, such as the absence of a bifurcation to the manubrium of the sternum, which have caused its position to be questioned."

In the light of presently available specimens, the character of the absence of the manubrial bifurcation is not valid. The bifurcations, although highly variable in development, are present to some degree in all species, although perhaps not in all specimens.

Procnias has the most distinctive and highly modified cotingid skull examined. A number of its features seem to be elaborations of lesser modifications present among the *Cotinga* group of skulls, but there is a significant gap

between the two types, with no even remotely intermediate form existing. A detailed comparative functional analysis may shed some light on the derivation of this type of skull.

Procnias Illiger 1811 (see Hellmayr, 1929: 237, for complete synonymy) is here designated the type and only genus of a new subfamily, Procniatinae, placed within the family Cotingidae. The genus may be closer to the Gymnoderinae and Cotinginae than to the Querulinae, some members of which it resembles only in size and color.

Subfamily QUERULINAE Swainson 1837
Lipauginae Sclater 1862
Cephalopterinae Reichenow 1914

The subfamily Querulinae was placed by Swainson with the flycatchers. On the transfer of Querula to the Cotingidae, it was united with the fruitcrows and their allies in the Gymnoderinae of Sclater. "These are exaggerated forms of the Cotingidae, in which development of colour, size, and ornamental appendages have been pushed to their extreme limits. Whether they should all stand together is doubtful, especially as regards. . . [Gymnoderus and Procnias] . . ." (Sclater, 1888: 394).

As reconstructed by Salvin and Godman (1891), the subfamily Querulinae consists of the fruitcrows (Querula, Pyroderus, and Haematoderus), capuchinbirds (Perissocephalus), and umbrellabirds (Cephalopterus). With the removal of Procnias and the restriction of Gymnoderinae to the type genus, the remaining birds are a much more

homogeneous group. Only the umbrellabirds are conspicuously ornamented.

Osteologically, Cephalopterus is most similar to Pyroderus. Querula and Haematoderus are each distinct, but are similar enough to be included in the same broad group. No skeleton of Perissocephalus was available for examination.

The subfamily Lipauginae, as conceived by Sclater, contained birds now placed in the genera Lipaugus, Rhytipterna, Laniocera, and Chirocylla. This group requires extensive investigation, as it seems to be an artificial assemblage of superficially similar birds, grouped together essentially by the possession of nonexaspidean tarsi and toes united to a degree intermediate between that of the cotingas and manakins.

Skulls of Rhytipterna are virtually indistinguishable from those of Sirystes, Myiarchus, and Eribates. The birds are similar in appearance, and the type of tarsal scutellation responsible for the placement of Rhytipterna outside of the Tyrannidae can be found among members of the tyrannid genera with similar skulls. The absence of any substantial unifying character with the Cotingidae requires that Rhytipterna be transferred to the Tyrannidae and placed near Myiarchus, which it most resembles.

Lipaugus skulls resemble most those of the larger fruitcrows. The same line of reasoning that I have

applied to Rhytipterna applies here, and Lipaugus is returned to the Querulinae, where it was originally placed by Swainson. It is interesting to note that Swainson (1862) considered Lipaugus more nearly related to Querula than to Rhytipterna. "It seems, therefore, that this resemblance between [Rhytipterna simplex and Lipaugus cinereaceus] must be looked upon as only analogical, seeing that the former bird, however disguised, has all the essential characters of the true tyrants, the strong and clasping scales of the tarsi alone excepting . . ." Rhytipterna has the margins of the plantar scutes recurved, forming a single row of conspicuous scutellations. This is a unique generic character.

Skeletons of Laniocera and Chirocylla have not been available for examination.

Subfamily TITYRINAE
Pearinae Swainson 1837
Tityrinae Gray 1841

The essentially tyranno-myiarchine nature of the tityrine skulls and the apparent divergence within the group creates a problem of allocation for which there are a number of possible solutions.

As mentioned earlier, the external appearances of the tityras and becards are quite distinct. The shape of the reduced ninth primary is different, in that in the tityras it is extremely narrow, and in the becards it is broad. Scutellation of the tarsal envelope also differs (see

caption, Figure 12). Finally, skulls of the becards differ less at the generic level than do the tityras at the specific level, while plumages differ in the reverse.

Differences between skulls of Erator and Platypsaris seem too insignificant to allow separation of the tityras and becards on the basis of cranial evidence alone, but separation of the becards (Pachyramphus and Platypsaris) as a separate subfamily, Pachyramphinae, might be advisable for the above listed reasons. The subfamily Tityrinae would then be restricted to the genera Tityra and Erator (Erator is often used in the literature for T. inquisitor, and in view of the relative breadth of the evolutionary gap between that species and T. semifasciata and cayana, as indicated by the associated modifications of the bill and nasal capsule, I believe the separation to be justified). In order to emphasize the distinctness of these two well-marked groups of tyrannoid genera from the remainder of the Cotingidae, should the above course of action be followed, it might be advisable to set them apart as a separate family, Tityridae.

The similarity of the skulls of the becards to those of the tyranno-myiarchine flycatchers is great enough to establish the probability of a closer relationship between these two groups than between the Tityrinae (s.l.) and the remainder of the Cotingidae. If further investigations

can establish a closer link between the becards and flycatchers than between the becards and tityras, a possible future course of action might be to unite the "Pachyramphinae" with the Tyrannidae, as a distinct subfamily, and to retain the Tityrinae (s.s.) at family rank.

The most logical action would seem to me to be to transfer tentatively the Tityrinae to the Tyrannidae, with two tribes, Tityrini and Pachyramphini, rather than to create a new family Tityridae. Retention of the Tityrinae among the Cotingidae, essentially on the largely discredited characters of the feet and legs, does not seem justified.

Subfamily ATTILINAE Sclater 1862

Salvin and Godman (1891: 132) give the following summary:

> The position of the Attilinæ has long been a matter of doubt, and it has been assigned to the families Tyrannidæ, Formicariidæ, and Cotingidæ. Sundevall placed it in the last named family, and in so doing, he was followed by Mr. Sclater, though in doubt. In this, we think, the last-named writer was justified, for the . . . [characters] are all suggestive of a different position from that now assigned to it. It is to be hoped that when the internal structure is examined, more satisfactory indications of the affinities of Attila will be revealed.

Neither Sclater nor Salvin and Godman suggested another position for the group, but Hellmayr (1929: 128) was of the opinion that Attila probably belonged in the Tyrannidae.

In general appearance, specimens of Attila are strongly reminiscent of the large ground-tyrants of the genus

Agriornis. The peculiarly compressed form of the elongate bill, with its strong terminal hook, is due in large part to modifications of the rhamphotheca, as it is in Agriornis.

The skull is essentially tyrannine, with a few characters in common with the fluvicoline skulls of the larger ground-tyrants. In themselves, Attila skulls represent a distinct type.

The Attilinae probably should be transferred to the Tyrannidae, retaining their status as a distinct subfamily.

Casiornis has usually been included in this subfamily. No skeletal specimen of this genus was available for examination.

Family RUPICOLIDAE
Rupicolinae Sclater 1862

The relationships of Rupicola have been long in doubt. The genus has been variously placed in the families Pipridae, Cotingidae, and Rupicolidae.

Gilliard (1962) was of the opinion that Rupicola is more closely related to Procnias in the Cotingidae than to the Pipridae. Moynihan (1963) has challenged Gilliard's interpretation of the differences between the behavior of Rupicola and the manakins. Cranial morphology tends to support Gilliard on the latter point but not on the relationship to Procnias.

As previously pointed out, skulls of both Procnias and

Rupicola are extremely specialized. Rupicola skulls have a number of individual features that occur in other large fruit-eating tyrannoids, but the combination of midifications is unique, as are some other features. Since there has been so far found among the Tyrannoidea no even remotely similar skull to serve as an intermediate "type" through which the Rupicola type of skull could be "derived," cranial morphology offers no clue as to where these unique birds could be placed within the Cotingidae, nor even evidence to support their inclusion within the family.

As the behavior of Rupicola is as much an extreme for the Cotingidae as that of the manakins, the same line of reasoning may apply, and until other evidence is forthcoming, the Rupicolidae probably should remain apart. If further evidence indicates that they should be included within the Cotingidae, they then should retain their earlier status as a separate subfamily, since there is a considerable morphological and behavioral hiatus between them and the three other equally distinct subfamilies of large fruit-eaters.

Phoenicircus is of uncertain position and has been sometimes considered allied to Rupicola. No skull of this genus has been available for examination.

Family PHYTOTOMIDAE
Phytotominae Swainson 1837

Kūchler (1936) conducted an extensive anatomical

investigation of Phytotoma, concluded that the genus was closely allied to the Cotingidae, and placed it within that family. Most modern systematists have not followed Küchler's recommendation and have maintained these highly modified birds as a separate family.

I have so far examined no skulls in the Tyrannoidea that approach those of Phytotoma in structure. Phytotoma skulls are every bit as distinct as the phytophagous habits of the birds would lead one to anticipate. Even if a common ancestry is assumed for the two families, there is evident an evolutionary gap great enough to justify family-level separation.

Family OXYRUNCIDAE
Oxyramphinae Swainson 1837
Oxyruncidae Hellmayr 1927

Since the study by Clark (1913) of a poorly preserved carcass of Oxyruncus, the tendency has been to place the sharpbills among the Tyrannidae.

Hayse (1965) found the humerus of Oxyruncus to be unique among the Tyrannoidea in the degree of deflexion of the deltoid crest and noted a resemblance to the humerus of Rhinocrypta.

The icteriod conformation of the skull, plus the long, well-developed mandibular retroarticular process (insertion for the M. depressor mandibulae), suggests the possibility of some degree of convergence with several of the icterids that utilize powerful "gaping" actions of the jaws either

in probing earth or moving aside ground debris in search of food (see Beecher, 1951; Zusi, 1959).

While the condition of the deltoid crest in Oxyruncus is not as extreme as that in the characteristic humerus of the weak-flying rhinocryptids, there exists the possible implication that Oxyruncus, whose habits are little known, might be to some extent a terrestrial "prober," searching for some of its food on the ground or possibly in rotten logs on the forest floor.

The skull provides no evidence for allying Oxyruncus with any tyrannoid examined. The uniqueness of the highly specialized skull argues against the inclusion of the genus in an otherwise so relatively homogeneous a family as the Tyrannidae.

SUMMARY AND CONCLUSIONS

1. A total of 1186 skulls of 224 species of 117 genera of the five closely related families that compose the New World Tyrannoidea has been examined in an attempt to clarify relationships among this difficult group of birds. One new subfamily, Procniatinae, has been erected in the Cotingidae to contain the bellbirds (Procnias).

2. The morphological features of the skull appear generally related to the external appearance, food preference, foraging habits, and breeding behavior of groups of tyrannoid birds, insofar as these features are presently known.

3. The skull, as a single character complex, seems to be a valid taxonomic character when related to other characters or groups of characters.

4. The level at which characters of the skull may be put to taxonomic use varies from group to group but is relatively constant within each group.

5. Skulls are generally more highly differentiated at lower taxonomic levels among groups of frugivorous tyrannoids than among the insectivorous forms.

6. Variation in characters of the feet and legs appear taxonomically significant only at a lower level (within any given group in which such differences occur) than the major

features of the skull.

7. As presently constituted, the Cotingidae and Tyrannidae merge insensibly *via* the insectivorous "cotingas." If family lines were drawn according to the criteria used here, rather than those of the feet and legs, the Cotingidae would be a less heterogeneous assemblage. Although more homogeneous than the Cotingidae, the Tyrannidae are heterogeneous enough to absorb the mourners, attilas, and becards without being noticeably affected.

8. The tityras appear to be an aberrant offshoot of the becards (or a "becardlike ancestor"). The Tityrinae seem to form a distinct "unit," but they resemble the remaining Cotingidae less than they do the Tyrannidae.

9. The mourners (*Rhytipterna*) are transferred to the Tyrannidae, near *Myiarchus*; transfer of the Attilinae to the Tyrannidae is recommended; removal of the Tityrinae from the Cotingidae is suggested, along with possibilities for their reallocation.

10. There appears to be a dichotomy among the skulls of the frugivorous cotingas, with the pihas, fruitcrows, and umbrellabirds in one group, and the cotingas, berry-eaters, bare-necked grackles, and possibly the bellbirds in the other.

11. A similar dichotomy exists among the Pipridae, with skulls of the typical, dimorphic manakins resembling most those of the cotingas (Cotinginae), and skulls of the

flycatcherlike nondimorphic manakins those of a few genera of smaller flycatchers.

12. The skull of the Enigma Manakin, Sapayoa aenigma, bears a striking resemblance to that of Smithornis in the Eurylaimidae. The possible inclusion of Sapayoa in the Eurylaimidae is worthy of investigation.

13. There is as great a morphological gap between skulls of Rupicola and the manakins as there appears to be between each and the Cotingidae in behavior, as far as the latter is known. Retention of the families Rupicolidae and Pipridae as distinct from the Cotingidae is recommended until more evidence is forthcoming.

14. Skulls of Oxyruncus and Phytotoma are each highly modified and resemble those of no other tyrannoids yet examined. Retention of the families Oxyruncidae and Phytotomidae is recommended.

15. Additional investigations of the nasal capsule and palatine process of the premaxilla may provide information of a fundamental nature that may further clarify the relationships of tyrannoid birds.

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APPENDIX I

TYRANNOID FORMS EXAMINED

The following is a list of tyrannoid species, skeletons of which were studied in this survey. Appended to each name is the number of skeletons examined. Genera are arranged alphabetically within each family. Allocations of genera are those of Hellmayr (1927, 1929).

TYRANNIDAE

- Aechmolophus
  - mexicanus 1
- Agriornis
  - livida 4
  - microptera 1
  - montana 1
- Arundinicola
  - leucocephala 4
- Blacicus
  - hispaniolensis 1
- Camptostoma
  - obsoletum 5
- Capsiempis
  - flaveola 2
- Cnemotriccus
  - fuscatus 6
  - poecilurus 2
- Cnipodectes
  - subbrunneus 1
- Colonia
  - colonus 7
- Colopteryx
  - galeatus 6
- Contopus
  - cinereus 11
  - fumigatus 3
  - lugubris 1
  - pertinax 4
  - sordidulus 15
  - virens 25
- Coryphotriccus
  - parvus 3
- Elaenia
  - [sp.] 2
  - albiceps 5
  - chiriquensis 2
  - fallax 3
  - flavogaster 14
  - frantzii 2
  - gaimardii 2
  - obscura 5
  - pallatangae 2
  - parvirostris 1
- Empidonax
  - [sp.] 1
  - atriceps 4
  - difficilis 8
  - flaviventris 12
  - fulvifrons 3
  - hammondii 4
  - minimus 11
  - oberholseri 3
  - traillii 7
  - virescens 9
  - wrightii 4
- Empidonomus
  - aurantioatro-cristatus 1
  - varius 5
- Entotriccus
  - striaticeps 1

APPENDIX II

NONTYRANNOID FORMS EXAMINED

The following is a list of nontyrannoid suboscine genera, skeletons of which were examined in this survey. Genera are arranged alphabetically within the families.

EURYLAIMIDAE
- Calyptomena
- Corydon
- Smithornis

RHINOCRYPTIDAE
- Pteroptochos
- Rhinocrypta
- Scytalopus

CONOPOPHAGIDAE
- Conopophaga
- Corythopis

FORMICARIIDAE
- Cercomacra
- Cymbilaimus
- Dysithamnus
- Formicarius
- Grallaria
- Gymnopithys
- Herpsilochmus
- Hylophylax
- Hypocnemis
- Microrhopias
- Myrmeciza
- Myrmerchilus
- Myrmotherula
- Neorhopias
- Phaenostictus
- Pyriglena
- Sakesphorus
- Schistocichla
- Taraba
- Thamnophilus

FURNARIIDAE
- Anabacerthia
- Anumbius
- Asthenes
- Automolus
- Carthiaxis
- Coryphistera
- Cranioleuca
- Furnarius
- Geositta
- Leptasthenura
- Lochmias
- Margarornis
- Ochetorhynchus
- Philydor
- Phleocrypta
- Premnoplex
- Pseudocolaptes
- Pseudoseisura
- Sclerurus
- Schizoeaca
- Synallaxis
- Syndactyla
- Upucerthia
- Xenops

DENDROCOLAPTIDAE

- Campylorhamphus
- Dendrocincla
- Dendroplex
- Drymornis
- Glyphorhynchus
- Lepidocolaptes
- Sittasomus
- Xiphocolaptes
- Xiphorhynchus

MENURIDAE

- Menura

VITA

Stuart Lawrence Warter was born on April 9, 1934, in New York, New York. He received his elementary and secondary education in Miami Beach, Florida. He entered the University of Miami in September, 1952, and received the degree of Bachelor of Science, cum laude, in June, 1956, and Master of Science in August, 1958. He entered Louisiana State University in September, 1958, where he was a Graduate Assistant in Zoology until June, 1962. He subsequently served as a Research Associate in Entomology from September, 1962, to September, 1964, and as an Instructor in Zoology from September, 1964, to June, 1965. He has held summer Instructorships at Northwestern State College, Natchitoches, Louisiana (1960), and Louisiana State University (1961, 1962). He became a candidate for the degree of Doctor of Philosophy in Zoology at Louisiana State University in May, 1963.

EXAMINATION AND THESIS REPORT

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Major Field: Zoology

Title of Thesis: The Cranial Osteology of the New World Tyrannoidea and its Taxonomic Implications

Approved:

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29 July 1965